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2.3. REPTILES AND AMPHIBIANS

Table 2-3 summarizes the species of reptiles and amphibians included in this section. For range maps, refer to the general references identified in the individual species profiles. The remainder of this section is organized by species in the order presented in Table 2-3. The availability of information in the published literature varies substantially among species, which is reflected in the profiles. The measures used to describe body length are included in each species profile. Body weight is reported as fresh wet weight (including the shell for turtles), unless otherwise noted.

Unlike birds and mammals for which a single common name usually covers all subspecies, many reptile and amphibian subspecies are recognized by different common names. For example, there are two subspecies of *Rana clamitans*: the green frog and the bronze frog (Section 2.3.7). There are four subspecies of *Terrapene carolina*: eastern box turtle, three-toed box turtle, Florida box turtle, and Gulf Coast box turtle (Section 2.3.3). In this case, other species exist that are also known as box turtles: the ornate and desert box turtles belong to the species *T. ornata*. For species that could be confused with other species unless a subspecies common name is used, we selected the common name of the most widespread subspecies to use in the tables and titles of the species profile. As with the other species in the Handbook, however, the profile covers all subspecies for the selected species that were represented in the literature reviewed.

In these profiles, we use the word hibernation for the period of dormancy that reptiles and amphibians undergo during winter, when they change their metabolism to accommodate the low (often near freezing) temperatures and lack of food (and oxygen). Use of the word for this group is controversial, however, because the word was developed initially to describe mammalian winter dormancy. Some investigators argue that a different word, brumation, should be established to describe the overwintering dormancy and associated metabolic changes for reptiles and amphibians (Hutchison, 1979). Others disagree, because significant physiological changes also occur in reptiles and amphibians during winter dormancy. They argue that, although the physiological changes are different from those in mammals, the word hibernation is a general term that does not specify what

Table 2-3. Reptiles and Amphibians Included in the Handbook

Order	Common name	Scientific name	Section
Chelydridae	snapping turtle	<i>Chelydra serpentina</i>	2.3.1
Emydidae	painted turtle	<i>Chrysemys picta</i>	2.3.2
	eastern box turtle^a	<i>Terrapene carolina carolina</i>	2.3.3
Colubridae	racer	<i>Coluber constrictor</i>	2.3.4
	northern water snake^a	<i>Nerodia sipedon sipedon</i>	2.3.5
Salamandridae	eastern newt	<i>Notophthalmus viridescens</i>	2.3.6
Ranidae	green frog^a	<i>Rana clamitans clamitans</i>	2.3.7
	bullfrog	<i>Rana catesbeiana</i>	2.3.8

^aAdditional subspecies also are included in the profile.

metabolic changes occur to allow overwintering in a dormant state (Gatten, 1987). We have chosen this latter interpretation for the Handbook.

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2.3.1. Snapping Turtle (snapping turtles)

Order Testudines, Family Chelydridae. Snapping turtles are among the largest of the freshwater turtles. They are characterized by large heads with powerful hooked jaws. There are only two species of this family in North America (the snapping turtle, including both the common and Florida snapping turtles, and the alligator snapping turtle).

Selected species

The snapping turtle (*Chelydra serpentina*) is primarily aquatic, inhabiting freshwater and brackish environments, although they will travel overland (DeGraaf and Rudis, 1983; Ernst and Barbour, 1972; Smith, 1961). There are two subspecies recognized in North America that are primarily distinguished by range: *C. s. serpentina* (the common snapping turtle, which is the largest subspecies, primarily occupies the United States east of the Rockies, except for the southern portions of Texas and Florida), and *C. s. osceola* (the Florida snapping turtle, found in the Florida peninsula) (Conant and Collins, 1991). In this profile, studies refer to the *serpentina* subspecies unless otherwise noted.

Body size. Adult snapping turtles are large, 20 to 37 cm in carapace length, and males attain larger sizes than females (Congdon et al., 1986; Ernst and Barbour, 1972; Galbraith et al., 1988). In a large oligotrophic lake in Ontario Canada, adult males averaged over 10 kg, whereas the females averaged 5.2 kg (Galbraith et al., 1988). In other populations, the difference in size between males and females often is less (Congdon et al., 1986; Galbraith et al., 1988; Hammer, 1969). They reach sexual maturity at approximately 200 mm in carapace length (Mosimann and Bider, 1960). The cool, short activity season in more northern areas results in slower growth rates and longer times to reach sexual maturity (Bury, 1979).

Habitat. In the east, snapping turtles are found in and near permanent ponds, lakes, and marshes. However, in the arid west, the species is primarily found in larger rivers, because these are the only permanent water bodies (Toner, 1960, cited in Graves and Anderson, 1987). They are most often found in turbid waters with a slow current (Graves and Anderson, 1987). They spend most of their time lying on the bottom of deep pools or buried in the mud in shallow water with only their eyes and nostrils exposed. Froese (1978) observed that young snapping turtles show a preference for areas with some obstructions that may provide cover or food.

Food habits. Snapping turtles are omnivorous. In early spring, when limited aquatic vegetation exists in lakes and ponds, they may eat primarily animal matter; however, when aquatic vegetation becomes abundant, they become more herbivorous (Pell, 1941, cited in Graves and Anderson, 1987). Young snapping turtles are primarily carnivorous and prefer smaller streams where aquatic vegetation is less abundant (Lagler, 1943; Pell, 1941, cited in Graves and Anderson, 1987). Snapping turtles consume a wide variety of animal material including insects, crustaceans, clams, snails, earthworms, leeches, tubificid worms, freshwater sponges, fish (adults, fry, and eggs), frogs and toads, salamanders, snakes, small turtles, birds, small mammals, and carrion and plant material including various algae (Alexander, 1943; Graves and Anderson, 1987; Hammer, 1969;

Punzo, 1975). Budhabatti and Moll (1988) observed no difference between the diets of males and females who fed at the surface, midpelagic, and benthic levels. Bramble (1973) suggested that the pharyngeal mechanism of feeding (i.e., drawing water with food objects into the mouth) prevents snapping turtles from ingesting food above the air-water interface.

Temperature regulation and daily activities. Snappers are most active at night. During the day, they occasionally leave the water to bask on shore, but basking is probably restricted by intolerance to high temperatures and by rapid loss of moisture (Ernst and Barbour, 1972). In a study in Ontario, Canada, Obbard and Brooks (1981) found that the turtles were active in the early morning and early evening and basked in the afternoon but were rarely active at night. Active turtles were found in deeper waters than inactive snappers (Obbard and Brooks, 1981). Cloacal temperatures of 18.7 to 32.6°C were reported for snapping turtles captured in the water in Sarasota County, Florida, between May and October (Punzo, 1975).

Hibernation. Snapping turtles usually enter hibernation by late October and emerge sometime between March and May, depending on latitude and temperature. To hibernate, they burrow into the debris or mud bottom of ponds or lakes, settle beneath logs, or retreat into muskrat burrows or lodges. Snapping turtles have been seen moving on or below the ice in midwinter. Large congregations sometimes hibernate together (Budhabatti and Moll, 1988; Ernst and Barbour, 1972).

Breeding activities and social organization. Mating occurs any time turtles are active from spring through fall, depending on latitude (Ernst and Barbour, 1972). Some investigators believe that male snapping turtles are territorial (Kiviat, 1980; Pell, 1941, cited in Galbraith et al., 1987), but Galbraith et al. (1987) doubts that males defend their home ranges against other males. Sperm may remain viable in the female for several years (Smith, 1956). Nesting occurs from late spring to early fall, peaking in June (Ernst and Barbour, 1972). Hammer (1969) observed that larger, older females nested earlier in the season than did smaller, younger ones. Females often move up small streams to lay eggs (Ewert, 1976, cited in Graves and Anderson, 1987). The nest site may be in the soil of banks or in muskrat houses but more commonly is in the open on south-facing slopes and may be several hundred meters from water (DeGraaf and Rudis, 1983). The turtle digs a 4- to 7-in cavity on dry land, preferably in sand, loam, or vegetable debris. The duration of incubation is inversely related to soil temperature (Ernst and Barbour, 1972; Yntema, 1978, cited in Graves and Anderson, 1987). In more northerly populations, hatchlings may overwinter in the nest (DeGraaf and Rudis, 1983).

Home range and resources. Most turtles stay primarily within the same marsh or in one general area from year to year ((Hammer, 1969; Obbard and Brooks, 1981). The summer home range includes a turtle's aquatic foraging areas, but females may need to travel some distance outside of the foraging home range to find a suitable nest site (DeGraaf and Rudis, 1983). Obbard and Brooks (1980) found that females tagged at their nesting site moved an average of 5.5 km (± 1.8 SD) from the nest site afterwards. Lonke and Obbard (1977) observed that 91.9 percent of the turtles in one population returned to the same nesting site a year after having been tagged there. Home ranges overlap both between and within sexes (Obbard and Brooks, 1981). Young snapping turtles use

different habitats than adults; they tend to remain in small streams until shortly before maturity, when they migrate to habitats preferred by adults (e.g., ponds, marshes, lakes) (Hammer, 1971; Minton, 1972, cited in Graves and Anderson, 1987).

Population density. The density of snapping turtles appears to be positively correlated with the productivity of the surface water body (e.g., density in a eutrophic surface water body is higher than in an oligotrophic lake) (Galbraith et al., 1988). Specific habitat characteristics and intraspecific interactions contribute to the variability of observed population densities in snapping turtles (Froese and Burghardt, 1975).

Population dynamics. Females do not begin laying eggs until age 6 to 19 yr depending on latitude and when they reach an appropriate size (approximately 200 mm carapace) (Galbraith et al. 1989; Mosimann and Bider, 1960). Males mature a few years earlier than females (see table). Females may lay one or two clutches per season (Minton, 1972, cited in Graves and Anderson, 1987). Clutch size increases with female body size; Congdon et al. (1987) calculated the relationship between clutch size (CS) and plastron length (PL in mm) for a population in southeastern Michigan:

$$CS = -21.227 + 0.242 PL, (r^2 = 0.409, n = 65).$$

Clutch size has also been positively correlated with latitude (Petokas and Alexander, 1980). Hammer (1969) found that mammalian predators destroyed over 50 percent of the turtle nests in a South Dakota marsh, and in undisturbed nests, hatchling success was less than 20 percent. Petokas and Alexander (1980) observed a 94 percent predation rate of nests under study in northern New York. Adult mortality is low, corresponding with the long lives exhibited by these turtles (see table).

Similar species (from general references)

- The alligator snapping turtle (*Macrochelys temminckii*) is much larger (16 to 68 kg; 38 to 66 cm carapace) than the common snapping turtle and is one of the largest turtles in the world. Its range is from northern Florida to east-central Texas and north in the Mississippi Valley.

General references

Conant and Collins (1991); DeGraaf and Rudis (1983); Ernst and Barbour (1972); Graves and Anderson (1987).

Snapping Turtle (*Chelydra serpentina*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (kg)	A M summer	10.5 ± 2.85 SD		Ontario, Canada/large oligotrophic lake	Galbraith et al., 1988	
	A F summer	5.24 ± 0.85 SD				
	J B summer	1.15 ± 0.80 SD				
	A M summer	5.52 ± 2.23 SD		Ontario, Canada/eutrophic pond	Galbraith et al., 1988	
	A F summer	5.03 ± 1.12 SD				
	J B summer	1.40 ± 0.20 SD				
	A M	4.16 ± 0.28 SE		Michigan	Congdon et al., 1986	
	A F	3.16 ± 0.20 SE				
	J B	0.80 ± 0.07 SE				
	at hatching	0.0057		NS	Ernst & Barbour, 1972	
Egg Weight (g)	at hatching	0.0089	7 - 15 5.7 - 13.8	NS	Ewert, 1979	
	mm carapace:					
	118	0.33		Massachusetts	Graham & Perkins, 1976	
	127	0.44				
	134	0.53				
	167	1.03				
	192	1.51				
	220	2,362				
Body Length (mm carapace)	age in years		54 - 66 83 - 108 124 - 145 146 - 184 177 - 211 204 - 238	Michigan	Gibbons, 1968	
	1	62 ± 4.5 SD				
	2	102 ± 5.8 SD				
	3	137 ± 9.4 SD				
	4	168 ± 14.2 SD				
	5	198 ± 13.7 SD				
	6	222 ± 12.9 SD				

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Snapping Turtle

Snapping Turtle (*Chelydra serpentina*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Metabolic Rate ($\text{IO}_2/\text{kg-d}$)	7.18 kg, rest 25°C	2.54				Lynn & von Brand, 1945	1
Metabolic Rate (kcal/kg-d)	A F basal A M basal	3.2 3.0				estimated	2
Food Ingestion Rate (g/g-d)	B summer		0.01 - 0.016		New York/captivity	Kiviat, 1980	
<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
adults & juveniles: plants animals		35 - 70 6 - 35			location not specified (% of diet; measure NS)	Smith, 1956	3
adults: fish vegetation clams mud & rocks		83.7 13.6 0.2 2.5			Tennessee/embayment (% wet volume; gastro- intestinal tract contents)	Meyers-Schoene & Walton, 1990	
adults & juveniles: (plants) algae (animals) crayfish fiddler crab sucker bullhead sunfish unknown fish (miscellaneous)		(36.5) 12.8 (54.1) 8.9 2.7 3.2 6.3 7.5 12.4 (9.4)			Connecticut/lakes, ponds, streams, swamps (% wet volume; stomach contents)	Alexander, 1943	

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Snapping Turtle

Snapping Turtle (*Chelydra serpentina*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Home Range Size (ha)	A M summer	0.7 ± 0.29 SD	0.24 - 1.3	Ontario, Canada/lake	Galbraith et al., 1987	
	A F summer	3.79 ± 1.46 SD	2.5 - 5.19	Ontario, Canada/lake	Obbard & Brooks, 1981	
	A M summer	3.21 ± 2.67 SD	0.95 - 8.38			
	A B summer	3.44 ± 2.18 SD				
	A M	8.9		New York/fresh tidal wetland	Kiviat, 1980	
	A F nonbreed	7.2				
Population Density (N/ha)	A M summer	1.5	1.0 - 4.9	Ontario, Canada/oligotrophic lake	Galbraith et al., 1987	4
	B B summer	2.3 ± 1.45 SD	40.3 - 95.0	oligotrophic waters	Galbraith et al., 1988	5
	B B summer	60.4	4.4 - 65.9	eutrophic pond	Galbraith et al., 1988	
	B B summer	29.3 ± 27.6 SD		eutrophic ponds (other studies)	Galbraith et al., 1988	
	A B summer	59		Tennessee/pond	Froese & Burghardt, 1975	
Clutch Size		49.0 27.9 ± 0.76 SE 16.6 ± 1.6 SD	31 - 87 12 - 41 14 - 20	South Dakota/marsh se Michigan/NS Florida/NS	Hammer, 1969 Congdon et al., 1987 Iverson, 1977	6
Clutches/Year		> 1	1 - 2	Indiana/NS NS/summarizing other studies	Minton, 1972 Ernst & Barbour, 1972	7
Days Incubation		105	90 - 119 67 - 73	Ontario, Canada/lake se Wisconsin/NS	Obbard & Brooks, 1981 Ewert, 1979	
Age at Sexual Maturity (yr)	F nesting	6 - 8		New York/NS	Pell, 1941	8
	F nesting M	9 - 10 4 - 5		Iowa/NS	Christiansen & Burken, 1979	
	F nesting	17 - 19	at least 14 to 15	Ontario, Canada/riverine, mixed forest	Galbraith et al., 1989	

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Snapping Turtle

Snapping Turtle (*Chelydra serpentina*)

<i>Population Dynamics</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Length at Sexual Maturity	A B	200 mm carapace		Quebec, Canada/NS	Mosimann & Bider, 1960	
	A B	145 mm plastron		Tennessee/NS	White & Murphy, 1973	9
Annual Mortality Rates (%)	A B		3 - 7	NS/NS	Galbraith & Brooks, 1987	10
Longevity (yr)			at least 24	Michigan/marsh	Gibbons, 1987	
			at least 19	South Carolina/river	Gibbons, 1987	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating	April early June mid-June	June mid-June	November end of June	depends on latitude New York Florida	Ernst & Barbour, 1972 Kiviat, 1980 Punzo, 1975	
Nesting	May late May early June	June early to mid-June mid-June	September late June end of June	depends on latitude northern New York South Dakota	Ernst & Barbour, 1972 Petokas & Alexander, 1980 Hammer, 1969	
Hatching	August late August	September	October early October	depends on latitude se Michigan	Ernst & Barbour, 1972 Congdon et al., 1987	
Hibernation	October late September mid-October		March-May mid-March early May	depends on latitude Iowa Ontario, Canada	Ernst & Barbour, 1972 Christiansen & Burken, 1979 Obbard & Brooks, 1981	

- 1 Cited in Sievert et al. (1988).
- 2 Estimated assuming temperature of 20°C, using equation 3-50 (Robinson et al., 1983) and body weights from Congdon et al. (1986), after subtracting 30 percent of body weight to eliminate the weight of the shell (Hall, 1924). More information on estimating energy budgets for reptiles is provided in Congdon et al. (1982).
- 3 Method of estimating percent diet not specified.
- 4 Summary of six field studies, including the author's.
- 5 Summary of data from various authors for eleven eutrophic ponds.
- 6 Cited in Petokas and Alexander (1980).
- 7 Cited in Graves and Anderson (1987).

Snapping Turtle (*Chelydra serpentina*)

- 8 Cited in Galbraith et al. (1989).
- 9 Cited in Bury (1979).
- 10 Cited in Frazer et al. (1991).

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Snapping Turtle

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2.3.2. Painted Turtle (pond and marsh turtles)

Order Testudines, Family Emydidae. Pond and marsh turtles (i.e., sliders, cooters, red-bellied turtles, and painted turtles) are small to medium-sized semiaquatic turtles well known for basking in the sun. Painted turtles are the most widespread of these in North America, ranging across the continent.

Selected species

The painted turtle (*Chrysemys picta*) is largely aquatic, living in shallow-water habitats, and is among the most conspicuous of the basking turtles. There are four subspecies in the United States (only one reaching slightly into Canada), distinguished by color variations, body size, and range: *C. p. picta* (eastern painted turtle; 11.5 to 15.2 cm; range Nova Scotia to Alabama), *C. p. marginata* (midland painted turtle; 11.5 to 14 cm; range southern Quebec and southern Ontario to Tennessee), *C. p. dorsalis* (southern painted turtle; 10 to 12.5 cm; range southern Illinois to the Gulf), and *C. p. bellii* (western painted turtle; the largest of the subspecies, 9 to 18 cm; range southwest Ontario and Missouri to the Pacific Northwest) (Conant and Collins, 1991). *C. p. dorsalis* is the smallest subspecies and also one of the smallest emydid turtles in North America (Moll, 1973). Hybridization occurs between subspecies in areas where their ranges overlap (e.g., *bellii* × *marginata* hybrids may occur in areas of Michigan) (Snow, 1980).

Body size. Painted turtles are medium-sized turtles (10 to 18 cm). Males are smaller than females; adult males average from 170 to 190 g, whereas adult females average from 260 to 330 g in some populations (Congdon et al., 1986; Ernst 1971b). In general, the shell comprises approximately 30 percent of the total wet weight of turtles of this size (Hall, 1924). Frazer et al. (1991) estimated a relationship between plastron length (PL in mm) and age (t in years) for a population in Michigan in the 1980's using von Bertalanffy growth equations:

$$PL = 111.8(1 - 0.792e^{-0.184t}) \quad \text{for males, and}$$

$$PL = 152.2(1 - 0.852e^{-0.128t}) \quad \text{for females.}$$

Congdon et al. (1982) reported a relationship between plastron length (PL in mm) and body weight (Wt in grams) for painted turtles:

$$\log_e(Wt) = -6978 + 2.645 \log_e(PL).$$

Eggs weigh 4 to 6 g, and neonates retain a large yolk mass that they draw on for the first few months of life (Cagle, 1954).

Habitat. Painted turtle habitat requirements include soft and muddy bottoms, basking sites, and aquatic vegetation (Sexton, 1959). Painted turtles prefer slow-moving shallow water such as ponds, marshes, ditches, prairie sloughs, spring runs, canals, and occasionally brackish tidal marshes (Conant and Collins, 1991). They frequent areas with floating surface vegetation for feeding and for cover (Sexton, 1959). These areas tend to

be warmer than more open water, which is important in the early fall as temperatures begin to drop (Sexton, 1959). For winter hibernation or dormancy, painted turtles seek deeper water (Sexton, 1959). If outlying marsh areas are dry during the summer, the turtles may return to the more permanent bodies of water sooner (McAuliffe, 1978). Painted turtles sometimes inhabit stagnant and polluted water (Smith, 1956).

Food habits. Painted turtles are omnivorous. Depending on habitat and on age, painted turtles may consume predominantly vegetation or predominantly animal matter. Marchand (1942, cited in Mahmoud and Klicka, 1979) found in one population that juveniles consumed approximately 85 percent animal matter and 15 percent plant matter, whereas the adults were primarily herbivorous, consuming 88 percent plant matter and 12 percent insects and amphipods. Knight and Gibbons (1968) found oligochaets, cladocera, dragonfly nymphs, lepidopteran larvae, and tendipedid larvae and pupae to dominate the animal component of the diet and filamentous algae to dominate the plant component of the diet in a population living in a polluted river in Michigan. Adult painted turtles in a Pennsylvania population were found to consume only 40 percent plant matter (Ernst and Barbour, 1972), whereas in a Michigan marsh and elsewhere, painted turtles of all ages apparently consumed 95 to 100 percent plant matter (Cahn, 1937, cited in Smith, 1961; Gibbons, 1967). Some carrion also may be consumed (Mount, 1975).

Temperature regulation and daily activities. Painted turtles are diurnal and usually spend their nights sleeping submerged (Ernst, 1971c). During the day, they forage in the late morning and late afternoon and bask during the rest of the day (Ernst, 1971c). Active feeding does not occur until water temperatures approach 20°C, and these turtles are most active around 20.7 to 22.4°C (Ernst, 1972; Ernst and Barbour, 1972; Hutchinson, 1979). Basking is most frequent in the spring, summer, and fall, but occasionally painted turtles bask during warm spells in the winter (Ernst and Barbour, 1972). Sexton (1959) divided the annual activity cycle of painted turtles into five parts: (1) the prevernal, which begins with the final melting of winter ice and lasts until late March, or when the turtles begin to move in mass out of the hibernation ponds; (2) the vernal, from late March to late May, when the submerged aquatic plants important to the turtles grow to the surface of the water (the initiation of feeding and mating activities and the emergence of the hatchling turtles from the nests of the previous year also occur during this season); (3) the aestival, extending from June through August, when the turtles forage, grow, nest, and return to their winter hibernation ponds; (4) the autumnal, including September through November or when a permanent ice cover forms; and (5) the winter season, which lasts while the water is permanently covered with ice.

Hibernation. Most painted turtles become dormant during the colder months but will become active during warm periods in the winter (Ernst and Barbour, 1972). *C. picta* usually hibernates in muddy bottoms of ponds (DeGraaf and Rudis, 1983). Taylor and Nol (1989) found painted turtles overwintering in an Ontario pond in areas with a mean water depth of 0.32 m (range 0.2 to 0.48 m), mean sediment depth of 0.79 m (0.5 to 0.95 m), and mean sediment temperature of 4.1°C (3 to 6°C). During hibernation, painted turtles shift toward more anaerobic metabolism, supported by glycolysis of liver and skeletal muscle glycogen (Seymour, 1982). After emerging from hibernation, the turtles convert the accumulated lactate to glucose in the liver (using aerobic metabolism) (Seymour, 1982).

Breeding activities and social organization. Mating usually occurs in spring and summer but may continue into the fall (Ernst, 1971c; Gibbons, 1968a; Gist et al., 1990). Nesting occurs somewhat later (Cagle, 1954; Ernst and Barbour, 1972; Moll 1973). Eggs are often laid in high banks (DeGraaf and Rudis, 1983). The species does not appear to be territorial and can be found in large aggregations, particularly at favorite basking sites (Ernst, 1971c).

Home range and resources. In spring, as the winter ice melts, many painted turtles move away from the ponds in which they hibernated to more shallow ponds and marshes with surface vegetation (Sexton, 1959). Movements averaging 60 to 140 meters characterized one population in Michigan (Sexton, 1959). The summer home range includes the painted turtle's foraging areas and basking sites. Females find nesting sites on dry land outside of the foraging range; Congdon and Gatten (1989) found nests to average 60 meters from the edge of a foraging marsh. Females initiate nesting migrations during daylight hours, and most finish their nests before dark on the same day (Congdon and Gatten, 1989). In winter, painted turtles generally move back to the deeper ponds for hibernation (DeGraaf and Rudis, 1983).

Population density. Reported densities range from 11.1/ha in Saskatchewan (MacCulloch and Secoy, 1983) to 830/ha in Michigan marshes (Frazer et al., 1991). Accurate censuses are difficult, however (Bayless, 1975), and the distribution of painted turtles in summer is highly clumped, corresponding to the patches of floating aquatic vegetation (Sexton, 1959).

Population dynamics. Sexual maturity is attained in about 2 to 7 years, depending on the sex and size of the turtle and growing season (Christiansen and Moll, 1973; Ernst and Barbour, 1972). Males reach sexual maturity 1 to a few years earlier than females (Moll, 1973). Once sexual maturity is reached, growth of painted turtles slows or essentially ceases (Ernst and Barbour, 1972). Older, larger females tend to produce larger clutch sizes and larger eggs than younger, smaller females (Mitchell, 1985). In more southerly populations, painted turtles produce more clutches annually with fewer eggs each than in more northerly populations (Moll, 1973; Snow, 1980; Schwarzkopf and Brooks, 1986). Predation causes most nest losses, usually within the first 2 days after laying (Tinkle et al., 1981). The duration of the incubation period depends on soil temperature, and hatchlings may overwinter in the nest in more northerly populations (Gibbons and Nelson, 1978).

Similar species (from general references)

Many species of pond and marsh turtles can be found in similar habitats; however, there are important dietary differences among species that can affect exposure to environmental contaminants, as described below. Size is listed according to carapace length, which is longer than plastron length.

cooters

- The Florida cooter (*Pseudemys floridana*) is larger (23 to 33 cm) than the painted turtle. The *floridana* subspecies ranges from the coastal plain of

Virginia to eastern Texas and north in the Mississippi Valley to southern Illinois, while the *peninsularis* subspecies is restricted to the Florida peninsula. The Florida cooter resides in permanent bodies of water. In their first year, young cooters feed on both aquatic plant and animal life; later they become totally herbivorous.

- The river cooter (*Pseudemys concinna*), composed of five subspecies, also is larger (23 to 33 cm) than the painted turtle. It inhabits coastal plains ranging from southeastern Virginia to Georgia, southeast into Florida, west into Texas and New Mexico, and north in the Mississippi Valley to southern Illinois. It is chiefly a resident of streams and relatively large lakes. In their first year, young river cooters are omnivorous; the adults are almost entirely herbivorous.
- The Texas river cooter (*Pseudemys texana*) (18 to 25.5 cm) prefers rivers but can be found in smaller creeks and ditches. Its range is restricted to most of central and southeastern Texas.

red-bellied turtles

- The Florida red-bellied turtle (*Pseudemys nelsoni*) is larger (20 to 31 cm) than the painted turtle and has a range in the Florida peninsula and panhandle. It can be found basking on logs over fresh to moderately brackish water, and it prefers abundant submerged aquatic vegetation, its principal food.
- The Alabama red-bellied turtle (*Pseudemys alabamensis*) is larger (23 to 33 cm) than the painted turtle and is found only in the lower portion of the Mobile Bay drainage in Alabama. It prefers fresh to moderately brackish water with abundant aquatic vegetation, its principal food.
- The red-bellied turtle (*Pseudemys rubriventris*) is much larger (25 to 32 cm) than the painted turtle and is found in the mid-Atlantic states and eastern Massachusetts.

sliders

- The pond slider (*Trachemys scripta*) is similar in size or a little larger (12 to 20 cm) than the painted turtle and has three subspecies ranging from southeastern Virginia to northern Florida and west to New Mexico. During the first year, pond sliders are principally carnivorous, consuming aquatic insects, crustaceans, molluscs, and tadpoles. As they mature, sliders become herbivorous, consuming a wide variety of aquatic plants.
- The big bend slider (*Trachemys gaigeae*) (12 to 20 cm) is similar to the pond slider in size and habits. It is abundant locally in its limited range along the upper Rio Grande and some of its tributaries.

General references

Behler and King (1979); Conant and Collins (1991); Congdon et al. (1986); Ernst and Barbour (1972); Moll (1973); Sexton (1959).

Painted Turtle (*Chrysemys picta*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A F	266.5 ± 60.1 SD	83.5 - 450.3 102.0 - 274.5	Pennsylvania (<i>picta</i> x <i>marginata</i>)	Ernst, 1971b	
	A M	189.1 ± 52.3 SD		Michigan	Congdon et al., 1986	
	A F A M J B	326.7 ± 4.95 SE 176.9 ± 1.92 SE 64.2 ± 1.59 SE	3.5 - 3.9	central Virginia (<i>picta</i>)	Mitchell, 1985	
	at hatching at hatching	3.7 ± 0.2 SD 4.1 ± 0.61 SD		Iowa	Ratterman & Ackerman, 1989	
Body Length (mm plastron)	A F	157 ± 2.6 SE	136 - 185 96 - 155	Wisconsin (<i>bellii</i>)	Moll, 1973	
	A M	132 ± 2.9 SE		Michigan	Congdon et al., 1986	
	(mm plastron)	125.1 ± 0.64 SE 99.9 ± 0.48 SE 65.0 ± 0.65 SE		Michigan	Congdon et al., 1986	
(mm carapace)	A F A M J B	134.2 ± 0.81 SE 109.7 ± 0.54 SE 71.5 ± 0.69 SE				
Egg Weight (g)	initial mass	6.17		Georgia (<i>dorsalis</i>)	Congdon & Gibbons, 1985	
	initial mass final mass	6.65 ± 0.67 SD 8.62 ± 1.06 SD		Iowa	Ratterman & Ackerman, 1989	
Growth Rate	J F - 1 yr J F - 2 to 3 yr J F - 4 to 5 yr J F - 6 to 7 yr A F - 8 to 12 yr A F - > 12 yr	35 mm/yr 19 - 20 mm/yr 12 mm/yr 8 - 10 mm/yr 3 - 6 mm/yr < 3 mm/yr		Quebec, Canada (<i>marginata</i>) (measured using plastron)	Christens & Bider, 1986	

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Painted Turtle

Painted Turtle (*Chrysemys picta*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>	
Metabolic Rate (IO ₂ /kg-d)	adults; 25°C land, rest	0.73 ± 0.44 SD			North Carolina	Stockard & Gatten, 1983	1	
	water, swim juv.; 25°C feeding 1-day fast 10-day fast 19-day fast	0.22 ± 0.32 SD 0.39 ± 0.68 SD 5.06 ± 0.42 SE 3.44 ± 0.29 SE 1.98 ± 0.13 SE 1.57 ± 0.19 SE			NS (<i>marginata</i>)	Sievert et al., 1988	2	
Metabolic Rate (kcal/d, averaged over 1 year)	J F - yr 1 J F - yr 3 J F - yr 5 J F - yr 7 A F - yr 9 A F - yr 11 A F - yr 13	0.06 0.30 0.53 0.77 1.12 1.23 1.28			Michigan (<i>marginata</i>)	Congdon et al., 1982	3	
Food Ingestion Rate (g/g-d)							4	
Water Ingestion Rate (g/g-d)	A B		up to 0.025		Wisconsin (<i>bellii</i>) (lab)	Trobec & Stanley, 1971	5	
	A B summer	0.02	0.016 - 0.022		Pennsylvania (lab)	Ernst, 1972	6	
Inhalation Rate (m ³ /kg-d)	A B resting	0.0025 ±0.0005 SE			NS (lab)	Milsom & Chan, 1986		
<i>Dietary Composition</i>		Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
all ages: plants			> 95			Michigan/marsh (% wet weight; stomach contents)	Gibbons, 1967	

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Painted Turtle

Painted Turtle (*Chrysemys picta*)

<i>Dietary Composition</i>		Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
all ages:						Michigan/polluted river	Knight & Gibbons, 1968	
plants		31.6	38.7					
animals		77.3	72.3			(% wet weight; stomach contents)		
Oligochaeta		-	30.0					
Cladocera		1.5	48.5					
Odonata nymphs		60.0	38.3					
Lepidoptera larvae		1.0	50.0					
Tendipedidae larva		30.8	7.7					
Tendipedidae pupae		36.7	10.0					
detritus		7.8	1.9					
adults:						Pennsylvania (<i>picta</i>)/NS	Ernst & Barbour, 1972	
snails			12.1					
amphipods			3.0					
crayfish			7.5			(% wet volume; stomach contents)		
insects			11.5					
fish			13.0					
other animals			14.1			season not specified		
algae			14.7					
vascular plants			24.1					
other plants			0.8					
<i>Population Dynamics</i>	Age/Sex Cond./Seas.	Mean		Range or (95% CI of mean)		Location/Habitat	Reference	Note No.
Movements (m)	A B spring A B summer A B fall	63 - 144 86 - 91 88 - 130		up to 301 up to 300 up to 336		Michigan (<i>marginata</i>)/NS	Sexton, 1959	7
Population Density (N/ha)	B B summer	11.1				Saskatchewan, Canada (<i>bellii</i>)/river	MacCulloch & Secoy, 1983	
	B B			98 - 410		Michigan (<i>marginata</i>)/ponds, marsh	Sexton, 1959	
	B B	590		240 - 941		Pennsylvania/pond, marsh	Ernst, 1971c	
	B B	828				Michigan/lake, marsh	Frazer et al., 1991	

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Painted Turtle

Painted Turtle (*Chrysemys picta*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Clutch Size		19.8	17 - 23	Saskatchewan, Canada (<i>bellii</i>)/creek	MacCulloch & Secoy, 1983	
		10.7	4 - 16	Wisconsin (<i>bellii</i>)/NS	Moll, 1973	
		7.6	2 - 11	Michigan (<i>marginata</i>)/NS	Congdon & Tinkle, 1982	
		4.8	2 - 9	Tennessee (<i>dorsalis</i> x <i>marginata</i>)/NS	Moll, 1973	
Clutches/Year		1 - 2	2	Ontario, Canada/NS	Schwarzkopf & Brooks, 1986	
		1 - 2	2	Michigan (<i>bellii</i> x <i>marginata</i>)/NS	Snow, 1980	
		> 2	3	Illinois (<i>bellii</i> x <i>marginata</i>)/kettle ponds	Moll, 1973	
		> 3	5	Tennessee, Louisiana (<i>dorsalis</i> and <i>d.</i> x <i>marginata</i>)/NS	Moll, 1973	
Days Incubation			65 - 80 60 - 65 72 - 99	se Pennsylvania/NS se Wisconsin/NS (natural) nw Minnesota/NS (natural)	Ernst, 1971c Ewert, 1979 Ewert, 1979	
Age at Sexual Maturity (yr)	F	5 - 6		New Mexico (<i>bellii</i>)/NS	Christiansen & Moll, 1973	
	M	3		Wisconsin (<i>bellii</i>)/NS	Christiansen & Moll, 1973	
	F	8		Pennsylvania (<i>picta</i>)/NS	Ernst & Barbour, 1972	
	M	4		Tennessee (<i>dorsalis</i> x <i>marginata</i>)/NS	Moll, 1973	
	F	6				
	M	5				
	F	4 - 5				
	M	2 - 3				

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Painted Turtle

Painted Turtle (*Chrysemys picta*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Length at Sexual Maturity (mm plastron)	M	90		northern Michigan (<i>marginata, dorsalis</i>)/NS	Cagle, 1954	
	F	120 - 130				
	M	70		southern Illinois (<i>marginata, dorsalis</i>)/NS	Cagle, 1954	
	F	120 - 125				
	M	123	88 - 170	New Mexico (<i>bellii</i>)/NS	Christiansen & Moll, 1973	
	F	150	132 - 205			
Annual Mortality Rates (%)	A F		0 - 14	Saskatchewan, Canada, MI, NY, NE/NS	Zweifel, 1989	8
	A M		2 - 46			
	A B		4 - 6	Virginia/NS	Mitchell, 1988	8
	J B	54				
Longevity	M		up to 31 yrs	Michigan/marsh	Frazer et al., 1991	
	F		up to 34 yrs			
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Mating	late April March	April - early May October	mid-June May	se Pennsylvania Michigan Ohio	Ernst, 1971c Gibbons, 1968a Gist et al., 1990	
Nesting	June June late May	June	July July late June	se Pennsylvania Illinois, Kansas se Michigan (<i>marginata</i>)	Ernst, 1971c Smith, 1956, 1961 Tinkle et al., 1981	
Hatching	September August	late summer	spring September	se Michigan (<i>marginata</i>) Illinois (<i>marginata</i>) Kansas (<i>bellii</i>)	Tinkle et al., 1981 Cahn, 1937 Smith, 1956	9
Hibernation	late October late October		late March April	se Michigan (<i>marginata</i>) Kansas (<i>bellii</i>)	Congdon et al., 1982 Smith, 1956	

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Painted Turtle

Painted Turtle (*Chrysemys picta*)

- 1 Average mass of test animals resting on land and in water = 215 g (79 to 395 g) and of test animals swimming and measured for existence metabolism = 143 g (79 to 297 g).
- 2 Average weight of juvenile turtles = 7.7 g.
- 3 Based on an annual energy budget estimated by the authors assuming that females lay one clutch of eggs per year after their seventh year.
- 4 See Chapters 3 and 4 for approaches to estimating food ingestion rates from metabolic rate and diet.
- 5 Uptake of water by turtles held in tap water.
- 6 Measured as evaporative water loss.
- 7 Spring: from hibernation to other ponds; summer: back to hibernation ponds; fall: to deep-water areas for hibernation.
- 8 Cited in Frazer et al., 1991.
- 9 Cited in Smith, 1961.

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2.3.3. Eastern Box Turtle (box turtles)

Order Testudines, Family Emydidae. Box turtles are the most terrestrial of the Emydid turtles, having close-fitting shells that have allowed them to adapt well to terrestrial life. They are found throughout the eastern and central United States and into the southwest. They are omnivorous.

Selected species

The eastern box turtle (*Terrapene carolina carolina*) ranges from northeastern Massachusetts to Georgia, west to Michigan, Illinois, and Tennessee (Conant and Collins, 1991). There are four subspecies of *T. carolina*, all found within the eastern United States: *T. c. carolina* (above), *T. c. major* (Gulf Coast box turtle; the largest subspecies, restricted to the Gulf Coast), *T. c. triunguis* (three-toed box turtle; Missouri to south-central Alabama and Texas), and *T. c. bauri* (Florida box turtle; restricted to the Florida peninsula and keys) (Conant and Collins, 1991).

Body size. The eastern box turtle is small, with adults ranging from 11.5 to 15.2 cm in length (plastron) and approximately 300 to over 400 g. Hatchlings weigh approximately 8 to 10 g. Turtles continue to grow throughout their lives; however, their growth rate slows after reaching sexual maturity (Ernst and Barbour, 1972), and growth rings are no longer discernable after 18 to 20 years (Stickel, 1978). Body fat reserves in a Georgia population averaged 0.058 to 0.060 g of fat per gram of lean dry weight from spring through fall (Brisbin, 1972).

Habitat. Typical box turtle habitats include open woodlands, thickets, and well-drained but moist forested areas (Stickel, 1950), but occasionally pastures and marshy meadows are utilized (Ernst and Barbour, 1972). In areas with mixed woodlands and grasslands, box turtles use grassland areas in times of moderate temperatures and peak moisture conditions; otherwise, they tend to use the more moist forested habitats (Reagan, 1974). Many turtles are killed attempting to cross roads, and fragmentation of habitat by roads can severely reduce populations (DeGraaf and Rudis, 1983; Stickel, 1978).

Food habits. Adult *T. carolina* are omnivorous (Ernst and Barbour, 1972). When young, they are primarily carnivorous, but they become more herbivorous as they age and as growth slows (Ernst and Barbour, 1972). They consume a wide variety of animal material, including earthworms, slugs, snails, insects and their larvae (particularly grasshoppers, moths, and beetles), crayfish, frogs, toads, snakes, and carrion; they also consume vegetable matter, including leaves, grass, berries, fruits, and fungi (DeGraaf and Rudis, 1983). A high proportion of snails and slugs may comprise the animal matter in the diet (Barbour, 1950), and seeds can become an important component of the plant materials in the late summer and fall (Klimstra and Newsome, 1960).

Temperature regulation and daily activities. The species is diurnal and spends the night resting in a scooped depression or form that the turtle digs in the soil with its front feet (Ernst and Barbour, 1972; Stickel, 1950). *T. carolina* are most active in temperate,

humid weather (Stickel, 1950). In the summer, they avoid high temperatures during midday by resting under logs or leaf litter, in mammal burrows, or by congregating in mudholes (Smith, 1961; Stickel, 1950). In the hottest weather, they may enter shaded shallow pools for hours or days (Ernst and Barbour, 1972). In the cooler temperatures, they may restrict their foraging activities to midday (Stickel, 1950). In the laboratory, locomotion is maximal between 24 and 32°C (Adams et al., 1989). In the field, their mean active body temperature is approximately 26°C (Brattstrom, 1965, cited in Hutchinson, 1979).

Hibernation. In the northern parts of its range (northeastern Massachusetts, Michigan, Illinois), the eastern box turtle enters hibernation in late October or November and emerges in April. In Louisiana, Penn and Pottharst (1940, cited in Ernst and Barbour, 1972) found that *T. c. major* hibernated when temperatures fell below 65°F. To hibernate, the box turtle burrows into loose soil and debris or mud of ponds or stream bottoms. Congdon et al. (1989) found a South Carolina population of box turtles to occupy relatively shallow burrows (less than 4 cm) compared with those occupied by box turtles in colder regions (up to 46 cm). Dolbeer (1971) found hibernacula of box turtles in Tennessee to be under 15.5 cm of leaf litter and 5.8 cm of soil on average. In southern states, during rainy and warm periods, box turtles may become active again (Dolbeer, 1971). In Florida, the box turtle may be active all year (Ernst and Barbour, 1972).

Breeding activities and social organization. Box turtles are solitary except briefly during the mating season. Individuals restrict their activities to a foraging home range, but home ranges of different individuals can overlap substantially (Stickel, 1950). Mating usually occurs in the spring but may continue into fall, and eggs are laid in late spring and summer (Ernst and Barbour, 1972). The female digs a 3- to 4-inch cavity in sandy or loamy soil in which she deposits her eggs and then covers the nest with soil. Nests tend to be constructed several hundred meters from the female's foraging home range in the warmer and drier uplands (Stickel, 1989). The duration of incubation depends on soil temperatures, and sometimes hatchlings overwinter in the nest. The young are semiaquatic but seldom seen (Smith, 1956).

Home range and resources. Measures of the foraging home range for box turtles range from .5 ha to just over 5 ha (Dolbeer, 1969; Schwartz et al., 1984). A female may need to search for suitable nest site (e.g., slightly elevated sandy soils) (Ernst and Barbour, 1972) outside of her foraging home range (Stickel, 1950). Winter hibernacula tend to be within the foraging home range (Stickel, 1989).

Population density. Population density varies with habitat quality, but studies linking density to particular habitat characteristics are lacking. In some areas, population densities have declined steadily over the past several decades (Schwartz and Schwartz, 1974; Stickel, 1978). Some investigators attribute the decline to increasing habitat fragmentation and obstacles (e.g., highways) that prevent females from reaching or returning from appropriate nesting areas (Stickel, 1978; DeGraaf and Rudis, 1983).

Population dynamics. Sexual maturity is attained at about 4 or 5 years (Ernst and Barbour, 1972) to 5 to 10 years of age (Minton, 1972, cited in DeGraaf and Rudis, 1983). One to four clutches may be laid per year, depending on latitude (Oliver, 1955, cited in

Moll, 1979; Smith, 1961). Clutch size ranges from three to eight eggs, averaging three to four in some areas (Congdon and Gibbons, 1985; Ernst and Barbour, 1972; Smith, 1956). Juveniles generally comprise a small proportion of box turtle populations, for example, 18 to 25 percent in one population in Missouri (Schwartz and Schwartz, 1974) and 10 percent in a study in Maryland (Stickel, 1950). Some individual box turtles may live over 100 years (Graham and Hutchinson, 1969, cited in DeGraaf and Rudis, 1983; Oliver, 1955, cited in Auffenberg and Iverson, 1979).

Similar species (from general references)

- The ornate box turtle (*Terrapene ornata ornata*) and the desert box turtle (*Terrapene ornata luteola*) are similar in size and habits to the eastern box turtle. They occur in the western, midwestern, and southern midwestern states. Preferred habitats include open prairies, pastureland, open woodlands, and waterways in arid, sandy-soil terrains. The ornate box turtle and desert box turtle forage primarily on insects but also on berries and carrion.

General references

Behler and King (1979); Conant and Collins (1991); DeGraaf and Rudis (1983); Ernst and Barbour (1972); Stickel (1950).

Eastern Box Turtle (*Terrapene carolina*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A F fall	381 ± 29 SE		Georgia (<i>carolina</i>), captive	Brisbin, 1972	1
	A M fall	398 ± 47 SE				
	A F spring	388 ± 29 SE		Georgia (<i>carolina</i>)	Brisbin, 1972	
	A M spring	369 ± 47 SE				
	A F	372		South Carolina	Congdon & Gibbons, 1985	
	at hatching	8.8 8.4		Florida (<i>major</i>) Indiana (<i>carolina</i>)	Ewert, 1979 Ewert, 1979	
	2 months	21		Tennessee	Allard, 1948	
	1.3 years	40				
	3.3 years	54				
Body Fat (g/g lean dry weight)	B fall B spring B summer	0.058 ± 0.014 SE 0.060 ± 0.016 SE 0.059 ± 0.006 SE		Georgia (<i>carolina</i>), captive	Brisbin, 1972	
Length	A F A at hatching	129 mm plastron 28 mm carapace	up to 198 mm carapace	South Carolina NS/NS NS/NS	Congdon & Gibbons, 1985 Oliver, 1955 Oliver, 1955	2 2
Egg Weight (g)		9.02 ± 0.17 SE	6 - 11	South Carolina NS/NS	Congdon & Gibbons, 1985 Ernst & Barbour, 1972	
Metabolic Rate (kcal/kg-d)	A F basal	5.4			estimated	3
Food Ingestion Rate (g/g-d)						4

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Eastern Box Turtle

Eastern Box Turtle (*Terrapene carolina*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat (measure)	Reference	Note No.
snails crayfish plants crickets unidentified seeds		60 15 12.5 7.5 5			Kentucky (<i>carolina</i>)/ Cumberland Mountains (% volume; stomach contents)	Barbour, 1950	
plant matter insects (adults) insects (larvae) seeds Gastropoda Isopoda Diplopoda Decapoda Annelida mammals reptiles birds	35 18 4 8 18 <1 3 2 1 2 1 3	39 12 5 16 6 5 2 2 1 <1 3 1	20 12 9 33 8 3 5 0 4 2 1 <1		Illinois (<i>carolina</i>)/forest, prairie (% wet volume; digestive tract)	Klimstra & Newsome, 1960	
<i>Population Dynamics</i>	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)		Location (subspecies)/Habitat	Reference	Note No.
Home Range Size (ha)	summer	0.46			Tennessee (<i>carolina</i>)/ woodland	Dolbeer, 1969	5
	B M B F	1.2 1.1			Maryland (<i>carolina</i>)/ bottomland forest	Stickel, 1989	5
	B M B F	5.2 5.1			Missouri (<i>triunguis</i>)/mixed woods, fields	Schwartz et al., 1984	5
Population Density (N/ha)		2.8 - 3.6			Tennessee/woodland	Dolbeer, 1969	
		17 - 35			Maryland (<i>triunguis</i>)/forest	Schwartz et al., 1984	

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Eastern Box Turtle

Eastern Box Turtle (*Terrapene carolina*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Clutch Size		3.4 ± 0.3 SE 4	2 - 7	South Carolina/NS Washington, DC/NS	Congdon & Gibbons, 1985 Smith, 1956	
Clutches/Year		1	up to 4	Florida/NS Illinois/NS	Oliver, 1955 Smith, 1961	6
Days Incubation		99	78 - 102 69 - 161	northwest Minnesota/(natural) Washington, DC/(natural)	Ewert, 1979 Ewing, 1933	7
Age at Sexual Maturity (yr)	B	4 - 5		NS/NS	Ernst & Barbour, 1972	
	B	5 - 10		NS/NS	Minton, 1972	8
Length at Sexual Maturity (mm carapace)	B		100 - 130	NS/NS	Oliver, 1955	2
Longevity (yr)		20	up to 80 up to 138	NS/NS captive	Nichols, 1939a Oliver, 1955	8 2
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Mating	June	spring	July	northern range ne Carolinas, Washington, DC	Ernst & Barbour, 1972 DeGraaf & Rudis, 1983; Smith, 1956	
Hatching	September August		October September	northern range ne Carolinas	Ernst & Barbour, 1972 DeGraaf & Rudis, 1983	
Hibernation	November October		April April	northern range Missouri (<i>triunguis</i>)	Ernst & Barbour, 1972 Schwartz & Schwartz, 1974	

1 Cited in Ernst and Barbour (1972).

2 Cited in Auffenberg and Iverson (1979).

3 Estimated assuming temperature of 20°C, using Equation 3-50 (Robinson et al., 1983) and body weights of Brisbin (1972) after subtracting 30 percent of the body weight to eliminate the weight of the shell (Hall, 1924).

4 See Chapters 3 and 4 for methods of estimating ingestion rates from metabolic rate and diet.

Eastern Box Turtle (*Terrapene carolina*)

- 5 Foraging home range; nest sites can be several hundred meters away from the foraging home range.
- 6 Cited in Moll (1979).
- 7 Cited in Ewert (1979).
- 8 Cited in DeGraaf and Rudis (1983).

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Eastern Box Turtle

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2.3.4. Racer (and whipsnakes)

Order Squamata, Family Colubridae. All racer snakes (*Coluber constrictor*) and whipsnakes (*Masticophis*) belong to the family *Colubridae*, along with 84 percent of the snake species in North America. Colubrids vary widely in form and size and can be found in numerous terrestrial and aquatic habitats. The more terrestrial members of this family also include some brown and garter snakes; lined snakes; earth snakes; hognose snakes; small woodland snakes; green snakes; speckled racer and indigo snakes; rat snakes; glossy snakes; pine, bull, and gopher snakes; kingsnakes and milk snakes; scarlet, long-nosed, and short-tailed snakes; ground snakes; rear-fanged snakes; and crowned and black-headed snakes (Conant and Collins, 1991).

Selected species

Racer snakes (*Coluber constrictor*) are slender and fast moving and are found in a wide variety of terrestrial habitats. They are one of the most common large snakes in North America (Smith, 1961). There are 11 subspecies in North America, limited to the United States and Mexico: *C. c. constrictor* (northern black racer; southern Maine to northeastern Alabama), *C. c. flaviventris* (eastern yellowbelly racer; Montana, western North Dakota, and Iowa south to Texas), *C. c. foxii* (blue racer; northwest Ohio to eastern Iowa and southeast Minnesota), *C. c. anthicus* (buttermilk racer; south Arkansas, Louisiana, and east Texas), *C. c. etheridgei* (tan racer; west-central Louisiana and adjacent Texas), *C. c. helvigularis* (brownchin racer; lower Chipola and Apalachicola River Valleys in Florida panhandle and adjacent Georgia), *C. c. latrunculus* (blackmask racer; southeast Louisiana along east side of Mississippi River to northern Mississippi), *C. c. mormon* (western yellow-bellied racer; south British Columbia to Baja California, east to southwest Montana, western Wyoming, and western Colorado), *C. c. oaxaca* (Mexican racer; south Texas and Mexico), *C. c. paludicola* (Everglades racer; southern Florida Everglades region and Cape Canaveral area), and *C. c. priapus* (southern black racer; southeastern states and north and west in Mississippi Valley).

Body size. Adult racer snakes are usually 76 to 152 cm in total length (Conant and Collins, 1991). Brown and Parker (1984) developed an empirical relationship between snout-to-vent length (SVL)ⁱ and body weight for male and female racers of the *mormon* subspecies in northern Utah:

$\text{weight (g)} = -100.80 + 2.93 \text{ SVL (cm)}$	females, ^j and
$\text{weight (g)} = -82.65 + 2.57 \text{ SVL (cm)}$	males.

The equations apply only over a limited range of body sizes (40 to 70 cm) where the relationship is approximately linear instead of exponential. Kaufman and Gibbons (1975)

ⁱMeasures of SVL exclude the tail. Fitch (1963) estimated that the tail measures 28 percent of the SVL of young females and 31 percent of the SVL of young males.

^jFemales collected when nonreproductive.

determined a relationship between length and weight for both sexes of a South Carolina population:

$$\text{weight (g)} = 0.0003 \text{ SVL (cm)}^{2.97 (\pm 0.15 \text{ 2SE})} \quad \text{both sexes.}^k$$

Racers from populations in the northeastern United States tend to be the largest, while those from the far west and south Texas are the smallest (Fitch, 1963). Just prior to egg-laying, the eggs can account for over 40 percent of a gravid female's body weight (Brown and Parker, 1984). At hatching, racers weigh about 8 or 9 g. Weight gain during the first year is rapid, with both sexes increasing their weight after hatching by approximately 3.2 times in the first year (Brown and Parker, 1984). One-year-old females nearly double their weight during their second year (Brown and Parker, 1984). By the time females are 3 years old (when most reach sexual maturity), they are 1.3 times heavier than the males (Brown and Parker, 1984).

Habitat. Racers can be found in moist or dry areas, abandoned fields, open woodlands, mountain meadows, rocky wooded hillsides, grassy-bordered streams, pine flatwoods, roadsides, and marshes from sea level to 2,150 m in elevation (Behler and King, 1979). Racers are partially arboreal (Behler and King, 1979; DeGraaf and Rudis, 1983). *C. c. constrictor* seems to prefer forest edges and open grassy, shrubby areas (Fitch, 1963, 1982). In autumn, most *C. constrictor* move into woodlands to find rock crevices in which to overwinter (Fitch, 1982).

Food habits. Racers are foraging generalists that actively seek their prey. Their varied diet includes small mammals (e.g., mice, voles), insects, amphibians (especially frogs), small birds, birds' eggs, snakes, and lizards (Brown and Parker, 1982; Fitch, 1963; Klimstra, 1959). In early spring, *C.c. flaviventris* feeds primarily on mammals and from May to October feeds primarily on insects (Klimstra, 1959). They often capture new prey before fully digesting previously captured prey (Fitch, 1982). Females, which are larger than males, tend to consume a higher proportion of vertebrate prey than do the males (Fitch, 1982). Males tend to spend more time climbing among foliage in low shrubs and trees and consuming insects (Fitch, 1982).

Temperature regulation and daily activities. *C. constrictor* is diurnal and spends a good portion of the daylight hours foraging (Vermersch and Kuntz, 1986). The species is fast moving and may be encountered in almost any terrestrial situation (Fitch, 1982). Hammerson (1987) observed California racers to bask in the sun after emerging from their night burrows or crevices until their internal body temperature reached almost 34°C, after which they would begin actively foraging. When temperatures are moderate, racers will spend much of their time during the day in the open above ground; at high temperatures, racers may retreat underground (Brown and Parker, 1982). Although racers are good climbers, they spend most of their time on the ground (Behler and King, 1979). When searching for food or being pursued, the racer snake will not hesitate to climb or swim (Smith, 1961).

^k95 percent confidence interval for constant (intercept in log-transform regression) = 0.00015 to 0.00058.

Hibernation. In fall, racers move to their hibernacula fairly directly and begin hibernation soon thereafter (Brown and Parker, 1982; Fitch, 1963). Racers hibernate in congregations of tens to hundreds of snakes (Brown and Parker, 1984), sometimes with copperheads and rattlesnakes, often using deep rock crevices or abandoned woodchuck holes (Parker and Brown, 1973). They are among the earliest snakes to emerge from hibernation (DeGraaf and Rudis, 1983).

Breeding activities and social organization. The species breeds in the spring or early summer. Racers defend home territories (DeGraaf and Rudis, 1983; Smith, 1956). Eggs are laid in the summer in rotting wood, stumps, decaying vegetable matter, or loose soil and hatch about 2 months later (Behler and King, 1979; DeGraaf and Rudis, 1983). More than one male may mate with one female in a breeding season. Eggs may double in size before hatching by absorbing water from the surrounding soil (Fitch, 1963).

Home range and resources. *C. c. constrictor* appears to have a definite home range (Smith, 1956) and requires large tracts of mixed old fields and woodlands (M. Klemens, pers. comm., cited in DeGraaf and Rudis, 1983). Fitch (1963) described four types of movement depending on the season and activity: (1) those in areas where hibernation occurs (e.g., rocky ledges), (2) seasonal migration between hibernation and summer ranges during spring and fall, (3) daily activities within a home range during the active season, and (4) wandering movements during which the racer shifts its activities.

Population density. Population densities of between 0.3 and 7 active snakes per hectare have been recorded in different habitats and areas (Fitch, 1963; Turner, 1977). Data on population densities are limited due to the difficulty in accurately censusing snakes.

Population dynamics. Male racers can reach sexual maturity by 13 to 14 months, whereas females tend not to mature until 2 or 3 years of age (Behler and King, 1979; Brown and Parker, 1984). Adult females produce at most a single clutch each year (some may reproduce only in alternate years) (Fitch, 1963). In general, the number of eggs in a clutch is proportional to the size of the female and ranges from 4 to 30 eggs (Fitch, 1963). Incubation lasts approximately 40 days to 2 months, depending on temperature (Behler and King, 1979; Smith, 1956). Juvenile snakes suffer higher mortality rates (e.g., 80 percent) than adult snakes (e.g., 20 percent) (Brown and Parker, 1984).

Similar species (from general references)

- The eastern coachwhip (*Masticophis flagellum flagellum*) (black phase) is similar in size and ranges from North Carolina and south Florida to Texas, Oklahoma, and Kansas.
- The western coachwhip (*Masticophis flagellum testaceus*) is similar in size to the racer. It ranges from western Nebraska south to Mexico.
- The central Texas whipsnake (*Masticophis taeniatus girardi*), Schott's whipsnake (*Masticophis taeniatus schotti*), and Ruthven's whipsnake

(Masticophis taeniatus ruthveni) are all similar in size to the racer and are restricted to southern Texas and northern Mexico.

- The Sonora whipsnake (*Masticophis bilineatus*) can be slightly larger (76 to 170 cm) than the racer and is found from Arizona southwest to New Mexico and Mexico.
- The striped racer (*Masticophis lateralis*) is also similar in size to the racer snake. It ranges from south-central Washington southeast in Great Basin to southern New Mexico and western and central Texas, south to west-central Mexico.
- The desert striped whipsnake (*Masticophis taeniatus taeniatus*) is similar to the central Texas whipsnake. It ranges from northern Texas and northern California to Washington state.

General references

Behler and King (1979); Brown and Parker (1984); Conant and Collins (1991); DeGraaf and Rudis (1983); Fitch (1963).

Racer Snake (*Coluber constrictor*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	males: yrs/mm SVL			Utah (<i>mormon</i>)	Brown & Parker, 1984	
	<1 266	8.3				
	1 420	27.0				
	2 486	41.0				
	3 520	49.1				
	4 541	53.4				
	5 564	60.4				
	6 573	61.2				
	females: yrs/mm SVL			Utah (<i>mormon</i>)	Brown & Parker, 1984	
	<1 272	8.8				
	1 430	28.4				
	2 524	51.6				
	3 575	66.2				
	4 599	71.4				
	5 620	79.4				
	6 632	84.0				
	males: yrs/mm SVL			Kansas (<i>flaviventris</i>)	Fitch, 1963	
	2 615	68.2				
	3 706	102.1				
	4 757	139.0				
	5 806	152.4				
	6 827	175.9				
	7 845	181.2				
	8 868	217.5				

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Racer Snake (*Coluber constrictor*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g) (continued)	females: yrs/mm SVL 2 644 3 810 4 866 5 914 6 965 7 974	83.5 149.4 212.3 209.6 245.9 251.3		Kansas (<i>flaviventris</i>)	Fitch, 1963	
	neonate 215 mm SVL	4.16	2.4 - 5.8	Kansas (<i>flaviventris</i>)	Fitch, 1963	
Egg Weight (g)	female size: 892 mm SVL 773 mm SVL	5.5 4.9	4.4 - 6.0 4.4 - 5.2	Kansas (<i>flaviventris</i>)	Fitch, 1963	
	size NS	7.8 ± 0.17 SE	5.9 - 10.8	Utah (<i>mormon</i>)	Brown & Parker, 1984	
Juvenile Growth Rate (g/d)	both sexes; 0 to 10 wks	0.116		Kansas (<i>flaviventris</i>)	Fitch, 1963	1
Body Temperature (°C)	A B summer	31.8 ± 0.20 SE	18.6 - 37.7	Utah (<i>mormon</i>)	Brown, 1973	2
	A B summer	26 - 27 (mode)	15.5 - 32.4	Kansas (<i>flaviventris</i>)	Fitch, 1963	
Metabolic Rate (kcal/kg-d)	M basal F basal	6.78 6.19			estimated	3
Food Ingestion Rate (g/g-d)	B B: spring through fall	0.02		Kansas (<i>flaviventris</i>)	Fitch, 1982	4

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Racer Snake (*Coluber constrictor*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
insects small mammals amphibians reptiles birds other	20 62 5 7 4 2	40 27 13 8 6 6	64 21 3 - 8 4		s Illinois/pastures, meadows (% volume; digestive tracts)	Klimstra, 1959	5
small mammals orthopterans lizards snakes misc. insects birds frogs		65.7 14.3 9.2 4.2 1.9 3.5 1.2			Kansas (<i>flaviventris</i>)/ locations throughout state (% wet weight; scats and stomach contents)	Fitch, 1963	
mice orthopterans lizards frogs snakes crickets		15.4 4.6 61.5 12.6 5.1 0.8			Kansas (<i>flaviventris</i>)/ woodland, grassland (% wet weight; stomach contents)	Fitch, 1963	
<i>Population Dynamics</i>	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)		Location (subspecies)/ Habitat	Reference	Note No.
Home Range Size (ha)	A F summer A M summer	1.8 3.0			Kansas (<i>flaviventris</i>)/ woodland, grassland	Fitch, 1963	
Population Density (N/ha)	A B summer B B	7.0 0.32			Kansas (<i>flaviventris</i>)/ upland prairie, weeds, grasses Utah (<i>mormon</i>)/desert shrub	Fitch, 1963 Brown & Parker, 1984	

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Racer

Racer Snake (*Coluber constrictor*)

<i>Population Dynamics</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)/ Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Clutch Size	average	16.8	7 - 31	NS (<i>constrictor</i>)/NS	Fitch, 1963	6
	average	12.6	7 - 21	NS (<i>priapus</i>)/NS	Fitch, 1963	6
	average	5.28 ± 0.24 SE	4 - 8	Utah (<i>mormon</i>)/desert shrub	Brown & Parker, 1984	
Clutches/Year		0.5	up to 1	Kansas (<i>flaviventris</i>)/ woodland, grassland	Fitch, 1963	
Days Incubation	summer	51	43 - 63	Kansas (<i>flaviventris</i>)/lab	Fitch, 1963	
	summer	45 - 50		Utah (<i>mormon</i>)/desert	Brown & Parker, 1984	
Age at Sexual Maturity	F M	2 - 3 years 13 - 14 months		Kansas (<i>flaviventris</i>)/ woodland, grassland	Fitch, 1963	
Annual Mortality Rates (%)	B 2 yrs B 3 - 6 yrs B 7 yrs	58 25 - 30 38		Kansas (<i>flaviventris</i>)/ woodland, grassland	Fitch, 1963	
Longevity (yr)	A B		up to 20	Utah (<i>mormon</i>)/cold desert shrub	Brown & Parker, 1982	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Mating	April	May	June	Kansas (<i>flaviventris</i>)	Fitch, 1963	
	May		early June	NS (<i>constrictor</i>)	DeGraaf & Rudis, 1983	
	April		May	Texas (<i>flaviventris</i>)	Vermersch and Kuntz, 1986	
Nesting	June		July	Virginia, Carolinas	Martof et al., 1980	
	June		early August	Texas (<i>flaviventris</i>)	Vermersch and Kuntz, 1986	
Hatching	late August		early September	Kansas (<i>flaviventris</i>)	Fitch, 1963	
		mid-late August		Utah (<i>mormon</i>)	Brown & Parker, 1982	

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Racer Snake (*Coluber constrictor*)

<i>Seasonal Activity</i>	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Hibernation	late November early October		early April early May	Kansas (<i>flaviventris</i>) Utah (<i>mormon</i>)	Fitch, 1963 Brown & Parker, 1982	

- 1 Ten-week period from hatching to hibernation.
- 2 Active snakes under natural conditions; cited in Brown and Parker (1982).
- 3 Estimated assuming temperature of 20°C using Equation 3-50 (Robinson et al., 1983) and body weights of 3-year-old snakes from Fitch (1963).
- 4 Author estimated that the snakes eat approximately four times their body weight over the 213-day active season from spring through fall.
- 5 Size of snakes not specified; captured within the range of *C. c. flaviventris* and *C. c. priapus*.
- 6 Author summarizing own work and unspecified other studies.

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2.3.5. Northern Water Snake (water snakes and salt marsh snakes)

Order Squamata, Family Colubridae. Water snakes and salt marsh snakes (genus *Nerodia*) belong to the family *Colubridae*, along with 84 percent of the snake species in North America. Colubrids vary widely in form and size and can be found in numerous habitats, including terrestrial, arboreal, aquatic, and burrowing. The more aquatic types of snakes in this family include water snakes, salt marsh snakes, swamp snakes, brown snakes, and garter and ribbon snakes (Conant and Collins, 1991).

Selected species

The northern water snake (*Nerodia sipedon sipedon*) is largely aquatic and riparian. It ranges from Maine and southern Quebec to North Carolina. It also inhabits the uplands of western North Carolina and adjacent portions of Tennessee and Virginia, and its range extends west to eastern Colorado (Conant and Collins, 1991). Three additional subspecies are recognized, distinguished by range and habitat: *N. s. pleuralis* (midland water snake; ranges from Indiana to Oklahoma and the Gulf of Mexico and south of the mountains to the Carolinas, preferring fast-moving streams), *N. s. insularum* (Lake Erie water snake; inhabits islands of Put-in-Bay, Lake Erie), and *N. s. williamengelsi* (Carolina salt marsh water snake; inhabits the Outer Bank islands and mainland coast of Pamlico and Core sounds, North Carolina) (Behler and King, 1979; Conant and Collins, 1991).

Body size. The northern water snake is typically 61 to 107 cm in total length (Conant and Collins, 1991). Island populations of the species tend to be larger than mainland ones (King, 1986). King (1986) estimated the relationship between snout-to-vent length (SVL)¹ and body weight for Lake Erie water snakes (*N. s. insularum*):

weight (g) = 0.0005 SVL (cm) ^{3.07}	all snakes;
weight (g) = 0.0009 SVL (cm) ^{2.88}	females; and
weight (g) = 0.0008 SVL (cm) ^{2.98}	males.

Kaufman and Gibbons (1975) determined a relationship between length and weight for both sexes of a South Carolina population:

weight (g) = 0.0004 SVL (cm) ^{3.15 (± 0.12 SE)}	all snakes
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(95% CI for intercept = 0.00015 to 0.0011). Immediately after emergence from hibernation, females begin to gain weight and continue gaining weight until giving birth in late summer. Weight loss associated with parturition in one population ranged from 28.2 to 45.5 percent of the female's weight just prior to parturition (King, 1986).

¹Measures of SVL exclude the tail. Kaufman and Gibbons (1975) estimated that the tail represents 21.8 percent (± 0.010 SE) of the total length of a female and 25.7 percent (± 0.006 SE) of the total length of a male.

Habitat. The northern water snake prefers streams but can be found in lakes and ponds and nearby riparian areas (King, 1986; Smith, 1961). In the Carolinas and Virginia, they can be found from mountain lakes and streams to large coastal estuaries (Martof et al., 1980). They are absent from water bodies with soft muddy bottoms which may interfere with foraging (Lagler and Salyer, 1945). In Lake Erie, *N. s. insularum* occurs in shoreline habitats where rocks or vegetation provide refugia (King, 1986).

Food habits. Northern water snakes consume primarily fish and amphibians and, to a lesser extent, insects and small mammals (Raney and Roecker, 1947; Smith, 1961). Diet varies according to the age (and size) of the snake and food availability (DeGraaf and Rudis, 1983). Young snakes forage in shallow riffles and cobble bars, primarily waiting for prey to move within range (letter from K.B. Jones, U.S. Environmental Protection Agency Environmental Monitoring Systems Laboratory, to Susan B. Norton, January 6, 1992). Tadpoles comprise a large proportion of the diet of young snakes^m in some areas (Raney and Roecker, 1947). Adults are strong swimmers and can swim and dive for fish midstream, often capturing large specimens (e.g., 20 to 23 cm brown trout; 19 cm bullhead; 20+ cm lamprey) (Lagler and Salyer, 1945). They also tend to consume bottom-dwelling fish species (e.g., suckers) (Raney and Roecker, 1947). In New York, Brown (1958) found that *N. s. sipedon* consumed the most food between June and August; they consumed little during the remaining months prior to hibernation.

Temperature regulation and daily activities. The northern water snake is active both day and night but is most active between 21 and 27°C (Brown, 1958; Smith, 1961). During the day, they are found in areas that provide basking sites and are not found in heavily shaded areas (DeGraaf and Rudis, 1983; Lagler and Salyer, 1945). They may become inactive and seek shelter, however, if temperatures exceed 27°C (Brown, 1958; Lagler and Salyer, 1945). They become torpid at temperatures less than 10°C (Brown, 1958).

Hibernation. In autumn, the *N. sipedon* leaves the aquatic habitats to overwinter in rock crevices or in banks nearby (DeGraaf and Rudis, 1983; Fitch, 1982).

Breeding activities and social organization. The northern water snake breeds primarily in early spring, and the young are born from late summer to fall (i.e., viviparous) (DeGraaf and Rudis, 1983). The rate of development before hatching is temperature dependent (Bauman and Metter, 1977).

Home range and resources. The northern water snake usually stays in the same area of a stream, in the same pond, or in an adjacent pond for several years (Fraker, 1970). Snakes along streams have larger home ranges than snakes in ponds and lakes (Fraker, 1970). Fraker (1970) found that for large ponds (e.g., 1,500 to 2,000 m²), the home range of an individual snake is essentially the entire pond. In fish hatcheries with smaller ponds, individual snakes frequent more than one pond (Fraker, 1970).

^mSnakes less than 36 cm in length for this example.

Population density. Population density estimates for water snakes usually are expressed relative to a length of shoreline. Values from 34 to 380 snakes per km of shoreline have been reported for streams and Lake Erie islands (see table).

Population dynamics. Northern water snakes reach sexual maturity at 2 or 3 years of age, with males generally maturing earlier and at a smaller size than females (Feaver, 1977, cited in King, 1986; King, 1986). Clutch sizes vary from 5 or 10 to 50 or 60 depending on location and on female size (see table). The proportion of females breeding in a given year increases with increasing female size, as does clutch size and offspring weight (King, 1986). King determined the relationship of litter size to female SVL for Lake Erie water snakes (*N. s. insularum*):

$$\text{litter size} = -12.45 + 0.41 \text{ SVL (cm)}.$$

Feaver (1977, cited in King, 1986) determined the relationship for a Michigan population:

$$\text{litter size} = -23.55 + 0.55 \text{ SVL (cm)}.$$

Females produce only one clutch per year (Beatson, 1976). Information on annual survivorship of juveniles or adults was not identified in the literature reviewed.

Similar species (from general references)

- The Mississippi green water snake (*Nerodia cyclopion*) can be slightly larger (76 to 114 cm) than the northern water snake and is found in quiet waters of the Mississippi Valley.
- The blotched water snake (*Nerodia erythrogaster transversa*) is larger than the northern water snake (76 to 122 cm) and is found in western Missouri and Kansas to northeastern Mexico.
- The northern copperbelly (*Nerodia erythrogaster neglecta*) is larger than the northern water snake (76 to 122 cm) and ranges from western Kentucky to southeastern Illinois and to Michigan.
- The redbelly water snake (*Nerodia erythrogaster erythrogaster*) of the midwestern United States is close in size to the water snake. It is best suited to swampy areas and sluggish streams.
- The yellowbelly water snake (*Nerodia erythrogaster flavigaster*) is found in the lower Mississippi Valley and adjacent areas. Like the redbelly, it is similar in size to the water snake and likely to be found in swampy areas and sluggish streams.
- The banded water snake (*Nerodia fasciata fasciata*) is similar in size, and its range includes the coastal plain, North Carolina to Mississippi.

- The broad banded water snake (*Nerodia fasciata confluens*) (56 to 90 cm) occurs in the Mississippi River delta region in marshes, swamps, and shallow waters, including brackish waters along the Gulf Coast.
- The Florida water snake (*Nerodia fasciata pictiventris*) is similar in size to the northern water snake and ranges from the extreme southeast of Georgia to the southern tip of Florida. It lives primarily in shallow freshwater habitats.
- Harter's water snake (*Nerodia harteri*) is relatively small (51 to 76 cm) and is found in central Texas.
- The diamondback water snake (*Nerodia rhombifer rhombifer*) can be slightly longer (76 to 122 cm) than the northern water snake and is more thick-bodied than most *Nerodia*. Its range extends south from the Mississippi Valley into Mexico.
- The Gulf salt marsh snake (*Nerodia clarkii clarkii*) inhabits the Gulf Coast from west-central Florida to southern Texas. It is abundant in coastal salt meadows, swamps, and marshes.
- The Atlantic salt marsh snake (*Nerodia clarkii taeniata*) is restricted to Volusia County along the Atlantic Coast of north Florida.
- The mangrove salt marsh snake (*Nerodia clarkii compressicauda*) is small (38 to 76 cm) and inhabits the mangrove swamps of Florida's lower coasts.

Dietary differences are evident among these species. Mushinsky et al. (1982) found in Louisiana forested wetlands that *N. erythrogaster* and *N. fasciata* change from a diet of fish to one dominated by frogs when they exceed an SVL of 50 cm. *N. rhombifer* and *N. cyclopion*, on the other hand, consume primarily fish throughout their lives, although the species and size composition of their diet changes as they grow larger (Mushinsky et al., 1982). As *N. rhombifer* exceeds 80 cm SVL, it begins to prey upon larger fish that occupy deeper open-water habitats. *N. cyclopion* eats a larger proportion of centrarchid fish as its body size increases. In a study of the diet of *N. rhombifer*, Plummer and Goy (1984) found a relationship between the SVL of the snakes and the standard length (SL) of the fish prey (defined as 80 percent of total length):

$$SL_{\text{fish}} \text{ (cm)} = -5.9 + 0.23 \text{ SVL}_{\text{snake}} \text{ (cm)} \quad \text{for males, and}$$

$$SL_{\text{fish}} \text{ (cm)} = -3.6 + 0.17 \text{ SVL}_{\text{snake}} \text{ (cm)} \quad \text{for females.}$$

The regression lines are not significantly different, however.

General references

Behler and King (1979); Conant and Collins (1991); DeGraaf and Rudis (1983); King (1986).

Water Snake (*Nerodia sipedon*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A B	207	up to 480	Kansas	Fitch, 1982	
	J B 1 yr	7.0 ± 2.3 SD	5.3 - 10.4	New York (<i>sipedon</i>)	Brown, 1958	
	J B 2 yr	29.0 (N = 2)	25.2 - 32.7			
	J M 3 yr	53.2 (N = 1)				
	A B 5 - 6 yr	210.0 ± 65 SD	114 - 255			
	neonate B	4.8	3.6 - 6.6	Ohio, Ontario (<i>insularum</i>)	King, 1986	
Length (mm)	A M	620 SVL		Ohio, Ontario (<i>insularum</i>)	King, 1989	1
	A F	745 SVL		New York (<i>sipedon</i>)	Brown, 1958	2
	J B 1 yr	285 total				
	J B 2 yr	496 total				
	J M 3 yr	607 total				
	A B 5 - 6 yr	868 total				
	neonate	181 SVL	125 - 210 SVL	Ohio, Ontario (<i>insularum</i>)	King, 1986	1
Juvenile Growth Rate (g/d)	J 1 yr	0.18 ± 0.08 SD	0.13 - 0.27	New York (<i>sipedon</i>)	Brown, 1958	
	J 2 yr	0.42	0.40 - 0.45			
	J 3 yr	0.80				
Metabolic Rate (IO ₂ /kg-d)	B resting:			Oklahoma, <i>Nerodia rhombifera</i> (similar species)	Gratz & Hutchinson, 1977	
	15°C	0.607 ± 0.035 SE	0.39 - 0.94			
	25°C	3.29 ± 0.10 SE	2.81 - 4.44			
	35°C	7.33 ± 0.23 SE	5.70 - 9.99			
Food Ingestion Rate (g/g-d)	J B 1 yr	0.088		New York (<i>sipedon</i>)	Brown, 1958	3
	J B 2 yr	0.043				
	J M 3 yr	0.043				
	A B 5 - 6 yr	0.061				
Surface Area (cm ²)	155 mm SVL	131.16		Arkansas, <i>Nerodia rhombifera</i> (similar species)	Baeyens & Rountree, 1983	

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Northern Water Snake

Water Snake (*Nerodia sipedon*)

Dietary Composition		Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat (measure)	Reference	Note No.
Esocidae Catostomidae Percidae Proteidae Cyprinidae Centrarchidae crawfish			7.0 22.5 15.7 51.9 1.5 0.3 1.5			Georgia/aquatic (NS) (% wet volume; stomach contents) season not specified	Camp et al., 1980	
trout non-trout fish unidentified fish Crustacea Amphibia birds & mammals unidentified			64 7 1 1 14 12 1			n lower Michigan/streams (% wet weight; stomach contents)	Alexander, 1977	4
minnows darters Amphibia sculpin (Cottidae) trout perch (Percopsis) game fishes (Perca) burbot (Lota) catfish (Ictaluridae)				9.1 1.4 52.8 2.2 2.8 14.1 17.4 0.3		n lower Michigan/lakes (% volume; stomach contents)	Brown, 1958	5
Population Dynamics	Age/Sex/ Cond./Seas.	Mean		Range		Location (subspecies)/ Habitat	Reference	Note No.
Population Density (N/km shore)	A B B B summer	138 34 - 41		22 - 381		Ohio, Ontario (<i>insularum</i>)/ Lake Erie islands Kansas (<i>sipedon</i>)/stream	King, 1986 Beatson, 1976	

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Northern Water Snake

Water Snake (*Nerodia sipedon*)

<i>Population Dynamics</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location (subspecies)/ Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Litter Size		11.8	4 - 24	Michigan (<i>sipedon</i>)/ponds, marshes	Feaver, 1977	6
		20.8 ± 8.2 SD	6 - 34	Ohio, Ontario (<i>insularum</i>)/ Lake Erie islands	Camin & Ehrlich, 1958	
		22.9	9 - 50	Ohio, Ontario (<i>insularum</i>)/ Lake Erie islands	King, 1986	
		33	13 - 52	Illinois (<i>pleuralis</i>)/NS	Smith, 1961	
Litters/Year		1		central Missouri (<i>sipedon</i>)/fish hatchery	Bauman & Metter, 1977	
		1		Kansas (<i>sipedon</i>)/stream	Beatson, 1976	
Days Gestation		58		central Missouri (<i>sipedon</i>)/fish hatchery	Bauman & Metter, 1977	
Age at Sexual Maturity (d)	F	34 mo		Michigan (<i>sipedon</i>)/ponds, marshes	Feaver, 1977	6
	M	23 - 24 mo				
	F	3 yrs		Ohio, Ontario (<i>insularum</i>)/ Lake Erie islands	King, 1986	
	M	2 yrs				
Length at Sexual Maturity (mm SVL)	F		476 - 649 375 - 425	Michigan (<i>sipedon</i>)/ponds, marshes	Feaver, 1977	6
	M					
	F	590		Ohio, Ontario (<i>insularum</i>)/ Lake Erie islands	King, 1986	
	M	430				
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Mating	mid-May	April - May May	mid-June	Kansas (<i>sipedon</i>) Michigan (<i>sipedon</i>) central Missouri (<i>sipedon</i>)	Smith, 1956 Feaver, 1977 Bauman & Metter, 1977	6

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Northern Water Snake

Water Snake (*Nerodia sipedon*)

<i>Seasonal Activity</i>	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Parturition	late August mid-August	late summer	September late September	Illinois (<i>sipedon</i>) Ohio, Ontario (<i>insularum</i>) Virginia, Carolinas (<i>sipedon</i>)	Smith, 1961 King, 1986 Martof et al., 1980	
Hibernation	mid-October November		mid-April late March	Ohio, Ontario (<i>insularum</i>) Michigan (<i>sipedon</i>)	King, 1986 Feaver, 1977	6

- 1 SVL = snout-to-vent length, which excludes the tail beyond the vent.
- 2 Total = total length, from nose to tip of tail.
- 3 Snakes in captivity; mean temperatures = 23°C. Snakes fed fish (one fed frogs).
- 4 Collected whenever they were found; thought to be active in area from May to September.
- 5 Months of collection and size of snakes not specified.
- 6 Cited in King (1986).

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Northern Water Snake

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2.3.6. Eastern Newt (salamanders)

Order Caudata, Family Salamandridae. *Notophthalmus*, the genus comprising the eastern newts, inhabits eastern North America. A different genus, *Taricha*, comprises the western newts along the Pacific coast of North America. Unlike other salamanders, the skin of newts is rough textured, not slimy. Eastern newts are primarily aquatic; western newts are terrestrial. The life cycle of eastern newts is complex. Females deposit their eggs into shallow surface waters. After hatching, the larvae remain aquatic for 2 to several months before transforming into brightly colored terrestrial forms, called efts (Healy, 1974). Postlarval migration of efts from ponds to land may take place from July through November, but timing varies between populations (Hurlbert, 1970). Efts live on land (forest floor) for 3 to 7 years (Healy, 1974). They then return to the water and assume adult characteristics. In changing from an eft to an adult, the newt develops fins and the skin changes to permit aquatic respiration (Smith, 1961). Occasionally newts omit the terrestrial eft stage, especially in the species located in the southeast coastal plain (Conant and Collins, 1991) and along the Massachusetts coast (Healy, 1974). These aquatic juveniles have the same adaptations (i.e., smooth skin and flattened tail) as the aquatic adults but are not sexually mature (Healy, 1973). Under favorable conditions, adults are permanently aquatic; however, adults may migrate to land after breeding due to dry ponds, high water temperatures, and low oxygen tension (Hurlbert, 1969). The life cycle of western newts does not include the eft stage (Conant and Collins, 1991).

Selected species

The eastern newt (*Notophthalmus viridescens*) has both aquatic and terrestrial forms. The aquatic adult is usually yellowish-brown or olive-green to dark brown above, yellow below. The land-dwelling eft is orange-red to reddish-brown, and its skin contains tetrodotoxin, a neurotoxin and powerful emetic. There are four subspecies of eastern newts: *N. v. viridescens* (red-spotted newt; ranges from Nova Scotia west to Great Lakes and south to the Gulf states), *N. v. dorsalis* (broken-striped newt; ranges along the coastal plain of the Carolinas), *N. v. louisianensis* (central newt; ranges from western Michigan to the Gulf), and *N. v. piaropicola* (peninsula newt; restricted to peninsular Florida) (Conant and Collins, 1991). Neotenyⁿ occurs commonly in the peninsula and broken-striped newts. In the central newt, neoteny is frequent in the southeastern coastal plain. In the red-spotted newt, neoteny is rare (Conant and Collins, 1991).

Body size. Adult eastern newts usually are 6.5 to 10.0 cm in total length (Conant and Collins, 1991). In North Carolina, *N. v. dorsalis* efts ranged from 2.1 to 3.8 cm snout-to-vent length (SVL), which excludes the tail, and adults ranged from 2.0 to 4.4 cm SVL (Harris, 1989; Harris et al., 1988). Healy (1973) found aquatic juveniles 1 year of age to range from 2.0 to 3.2 cm SVL. Adult eastern newts weigh approximately 2 to 3 g (Gill, 1979; Gillis and Breuer, 1984), whereas the efts generally weigh 1 to 1.5 g (Burton, 1977; Gillis and Breuer, 1984).

ⁿNeotenic newts are mature and capable of reproduction but retain the larval form, appearance, and habits (Conant and Collins, 1991).

Habitat. Larval and adult eastern newts are found in ponds, especially those with abundant submerged vegetation, and in weedy areas of lakes, marshes, ditches, backwaters, and pools of shallow slow-moving streams or other unpolluted shallow or semipermanent water. Terrestrial efts inhabit mixed and deciduous forests (Bishop, 1941, cited in Sousa, 1985) and are found in moist areas, typically under damp leaves, brush piles, logs, and stumps, usually in wooded habitats (DeGraaf and Rudis, 1983). Adequate surface litter is important, especially during dry periods, because efts seldom burrow (Healy, 1981, cited in Sousa, 1985).

Food habits. Adult eastern newts are opportunistic predators that prey underwater on worms, insects and their larvae (e.g., mayfly, caddisfly, midge, and mosquito larvae), small crustaceans and molluscs, spiders, amphibian eggs, and occasionally small fish. Newts capture prey at the surface of the water and on the bottom of the pond, as well as in the water column (Ries and Bellis, 1966). The shed skin (exuvia) is eaten and may comprise greater than 5 percent of the total weight of food items of both the adult and eft diets (MacNamara, 1977). Snails are an important food source for the terrestrial eft (Burton, 1976). Efts feed only during rainy summer periods (Behler and King, 1979; Healy, 1973). Healy (1975) noted that in late August and September, efts often were found clustered around decaying mushrooms feeding on adult and larval dipterans. In a northern hardwood hemlock forest in New York, MacNamara (1977) found that most prey of adult migrants and immature efts were from the upper litter layer, soil surface, or low vegetation.

Temperature regulation and daily activities. Adult newts are often seen foraging in shallow water, and efts are often found in large numbers on the forest floor after it rains (Behler and King, 1979). Efts may be found on the open forest floor even during daylight hours (Conant and Collins, 1991), but they rarely emerge if the air temperature is below 10°C (Healy, 1975).

Hibernation. Most adults remain active all winter underwater on pond bottoms or in streams (DeGraaf and Rudis, 1983). Some adults overwinter on land (Hurlbert, 1970) and migrate to ponds during the spring to breed (Hurlbert, 1969). If the water body freezes to the bottom, adults may be forced to hibernate on land or to migrate to another pool (Smith, 1956). Efts hibernate on land, burrowing under logs and debris. Hurlbert (1969) observed that efts migrated to ponds for the first time in the spring and fall.

Breeding activities and social organization. In south-central New York, breeding takes place in late winter or early spring, usually in lakes, ponds, and swamps (Hurlbert, 1970). Ovulation and egg deposition occur over an extended period (McLaughlin and Humphries, 1978). Females overwintering on land can store sperm for at least 10 months (Massey, 1990). Spawning underwater, the female deposits eggs singly on leaves of submerged plants, hiding and wrapping each in vegetation (Gibbons and Semlitsch, 1991; Smith 1956). The time to hatching depends on temperature (DeGraaf and Rudis, 1983). Smith (1961) found typical incubation periods to be 14 to 21 days in Illinois, whereas the incubation period observed by Behler and King (1979) was 21 to 56 days.

Growth and metamorphosis. In late summer or early fall, the larvae transform into either aquatic juveniles or terrestrial efts (Behler and King, 1979). Harris (1987) showed

that low larval density stimulated neoteny in larvae under experimental conditions. Larval growth rates were higher in ponds with low larval densities (Harris, 1987; Morin et al., 1983). Growth rates for aquatic juveniles are highest in the spring; however, maximum seasonal growth for the terrestrial eft occurs between June and September when the temperature is optimal for active foraging (Healy, 1973).

Home range and resources. For adult newts, Bellis (1968) found the mean distance between capture and recapture sites to be about 7 m, indicating small home ranges. Harris (1981, cited in DeGraaf and Rudis, 1983) did not find any defined home range or any territoriality for males. Most efts around a pond in Pennsylvania remained within 1.5 m of the shore (Bellis, 1968). Healy (1975) estimated the home range for terrestrial efts in a Massachusetts woodland to be 270 m² and located approximately 800 m from the ponds where the adults and larvae were located.

Population density. Populations of aquatic adults may reach high local densities, whereas terrestrial efts exhibit lower population densities. Recorded population densities for terrestrial efts range from 34 per hectare (ranging from 20 to 50 efts per hectare) in a North Carolina mixed deciduous forest (Shure et al., 1989) to 300 per hectare in a Massachusetts woodland (Healy, 1975). Harris et al. (1988) observed a density of 1.4 adult newts per m² (14,000 adult newts per hectare) in a shallow pond in North Carolina in the winter, whereas the summer population density was only 0.2 adults per m² (2,000 adults per hectare).

Population dynamics. Many populations of the eastern newt reach sexual maturity when the eft stage returns to the water and changes to the adult form (Healy, 1974). However, under certain conditions such as low larval density, most of the larvae present have been shown to metamorphose directly into adults or even into sexually mature larvae (Harris, 1987). In experimental ponds, densities of 22 larvae per m² resulted in metamorphosis to eft by the majority, while a density of 5.5 larvae per m² resulted in metamorphosis directly to the adult form or sexual maturation without metamorphosis (Harris, 1987). Adult density also influences reproduction. Morin et al. (1983) found that doubling adult density resulted in a reduction of offspring produced to one-quarter that produced by adults at the lower density (i.e., from 36 offspring per female in tanks containing 1.1 females per m² to 9.7 offspring per female in tanks containing 2.2 females per m²). The adult life expectancy noted by Gill (1978b) was 2.1 breeding seasons for males and 1.7 breeding seasons for females. Amphibian blood leeches (ectoparasites) are likely to be a primary source of mortality for adults; they also prey directly on larvae (Gill, 1978a).

Similar species (from general references)

- The black-spotted newt (*Notophthalmus meridionalis*) is similar in size (7.5 to 11.0 cm) to the eastern newt. It has large black spots and is found in south Texas in ponds, lagoons, and swamps. There is no eft stage.
- The striped newt (*Notophthalmus perstriatus*) is smaller (5.2 to 7.9 cm) than the eastern newt and ranges from southern Georgia to central Florida. It is found in almost any body of shallow, standing water.

- The western newts (*Taricha*) are found along the Pacific coast. They do not undergo the eft stage but rather transform into land-dwelling adults that return to the water at breeding time.
- Other small salamanders are similar but vary by having slimy skin and conspicuous costal grooves. They differ in life history, however; in the family *Plethodontidae*, all are lungless and breathe through thin, moist skin. Many are completely terrestrial.

General references

Behler and King (1979); Conant and Collins (1991); DeGraaf and Rudis (1983); Hurlbert (1969); Smith (1961).

Eastern Newt (*Notophthalmus viridescens*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	adult:					
	B	2.24 ± 0.71 SD	1.12 - 3.52	New York	Gillis & Breuer, 1984	
	F prebreed	3.05 ± 0.06 SE		Virginia	Gill, 1979	
	F postbreed	2.49 ± 0.06 SE				
	M prebreed	2.49 ± 0.03 SE				
	M postbreed	2.76 ± 0.03 SE				
	B spring	1.71 ± 0.43 SD		Massachusetts	Pitkin, 1983	
	B summer	2.13 ± 0.44 SD				
	B winter	1.94 ± 0.33 SD				
	B fall	1.63 ± 0.28 SD				
	larvae:					
	12.8 mm SVL	0.04 ± 0.025 SD		South Carolina	Taylor et al., 1988	
	21.9 mm SVL	0.54 ± 0.167 SD				
	eft:					
	B	1.10 ± 0.40 SD	0.42 - 1.82	New York	Gillis & Breuer, 1984	
	B	1.45		New Hampshire (<i>viridescens</i>)	Burton, 1977	
	B summer	1.23	0.63 - 2.17	New York	Stefanski et al., 1989	

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Eastern Newt

Eastern Newt (*Notophthalmus viridescens*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Length (mm SVL)	adult: M	35.0	24 - 44	North Carolina (<i>dorsalis</i>)	Harris et al., 1988	
	F	35.0	20 - 42			
	B summer	38.9	33 - 48	New York	MacNamara, 1977	
	juvenile: B spring	26.1 ± 0.35 SE	20 - 32	Massachusetts (<i>viridescens</i>)	Healy, 1973	
	larvae: B spring B fall	12.3 19.2		s Illinois	Brophy, 1980	
	eft: B (mm total)	50.4 ± 0.5 SE		North Carolina (<i>dorsalis</i>)	Harris et al., 1988	
	B spring	20.5		Massachusetts (<i>viridescens</i>)	Healy, 1973	
	B summer	32.7	18 - 41	New York	MacNamara, 1977	
	high density: -> efts -> adults -> neonates	0.00310 0.00421 0.00536		North Carolina high density: 55,000/ha	Harris, 1987	1
	low density: -> efts -> adults -> neonates	0.00635 0.00685 0.00676		low density: 220/ha		1
Metabolic Rate (IO_2 /kg-d)	efts at 15°C: resting active	1.47 4.27		New York	Stefanski et al., 1989	

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Eastern Newt

Eastern Newt (*Notophthalmus viridescens*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Metabolic Rate (kcal/kg-d)	basal:					
	A M postbreed	16.2			estimated	2a
	A F postbreed	16.7			estimated	2b
	larvae (12.8 mm)	43.5			estimated	2c
	eft (71.0 mm)	20.1				
Food Ingestion Rate (g/g-d)						3
Surface Area (cm ²)	A M A F	17 15			estimated	4

<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location (subspecies)/ Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
aquatic adults:							
Ephemeroptera		7.5	7.5				
Odonata		31.9	1.9				
Lepidoptera		13.7	0.9				
Diptera		5.8	0.3				
other insects		9.9	0.6				
Cladocerans		5.1	84.1				
Amphipoda		5.6	3.1				
Pelycepod		6.2	1.5				
<i>N. viridescens</i>							
larvae		11.4	0.0				
other		3.2	0.1				

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Eastern Newt

Eastern Newt (*Notophthalmus viridescens*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat (measure)	Reference	Note No.
efts: Basommatophora Stylommatophora Acari Collembola Thysanoptera Homoptera Coleoptera adult Coleoptera larvae Lepidoptera larvae Diptera adult Diptera larvae Hymenoptera adult		5.5 18.3 13.8 10.4 3.4 4.7 2.3 3.5 7.9 9.7 10.6 5.8			New York/leaf litter surface in forest (% dry weight; stomach contents)	MacNamara, 1977	
larvae: Zygoptera (Odonata) Chironomidae (Diptera) Cladocera Ostracoda Hyallela azteca (Amphipoda) Sphaerium sp. (Pelycepoda) Planorbidae (Gastropoda) Rhizopoda (Protozoa)		0.8 16.2 12.7 5.3 55.1 9.4 0.5 0.01			New Hampshire (<i>viridescens</i>)/small oligotrophic lake (% wet weight; stomach and gut contents)	Burton, 1977	

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Eastern Newt

Eastern Newt (*Notophthalmus viridescens*)

<i>Population Dynamics</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)/ Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Home Range Size	eft: B	0.0087 ha	0.0028 - 0.0153	Massachusetts (<i>viridescens</i>)/ oak/pine forest	Healy, 1975	5
	adult: summer	6.86 m		Pennsylvania (<i>viridescens</i>)/pond	Bellis, 1968	
Population Density (N/ha)	A B entire lake	130 - 173	20 - 50	New Hampshire (<i>viridescens</i>)/small oligotrophic lake	Burton, 1977	
	A B fringe only	50 - 2,600				
	A winter	50,000 ± 9,000 SE		North Carolina (<i>dorsalis</i>)/ shallow pond	Harris et al., 1988	
	A summer	3,000 ± 1,000 SE				
	eft spring	300		Massachusetts (<i>viridescens</i>)/ oak/pine forest	Healy, 1975	
	eft summer	34		North Carolina (<i>viridescens</i>)/mixed deciduous forest	Shure et al., 1989	
	larvae spring	21,000		South Carolina/pond, wetland	Taylor et al., 1988	
Clutch Size (eggs)	larvae spring summer fall	65,000 ± 15,000 SE 25,000 ± 5,000 SE 10,000 ± 3,000 SE	0 - 350,000	North Carolina (<i>dorsalis</i>)/ shallow pond	Harris et al., 1988	
Days to Hatching		14 - 21 21 - 56		Illinois/NS NS/NS	Smith, 1961 Behler & King, 1979	

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Eastern Newt

Eastern Newt (*Notophthalmus viridescens*)

<i>Population Dynamics</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)/ Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Age at Metamorphosis	larvae -> eft	2 - 3 mo 6 mo		Illinois (<i>louisianensis</i>)/NS Massachusetts (<i>viridescens</i>)/inland ponds South Carolina/ponds	Smith, 1961 Healy, 1974 Gibbons & Semlitsch, 1991	
	eft -> adult	1 - 3 yrs				
Age at Sexual Maturity	3 - 7 years eft	5 - 6 yrs	4 - 8	Massachusetts (<i>viridescens</i>)/inland ponds	Healy, 1974	
	no eft stage	2 yrs		coastal ponds		
Annual Mortality Rates (%)	A F A M	54.1 - 59.5 45.8 - 53.1		Virginia/mountain ponds	Gill, 1978a	
Longevity (breeding seasons)	A F A M	1.7 2.1		Virginia/mountain ponds	Gill, 1978b	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/Laying	February - March		April - May	South Carolina	Gibbons & Semlitsch, 1991	
	April		June	North Carolina	Harris et al., 1988	
Hatching	June			Virginia	Gill, 1978a	
	late April			North Carolina	Harris et al., 1988	
		spring		NS	Behler and King, 1979	

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Eastern Newt

Eastern Newt (*Notophthalmus viridescens*)

<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Metamorphosis to eft	June		September	South Carolina	Gibbons & Semlitsch, 1991	
	mid-August		late November	Virginia	Gill, 1978a	
	mid-July	August - Sept.	early November	New York	Hurlbert, 1970	
Fall Migration (of adults to hibernaculae)	August - Sept.		November	Virginia	Gill, 1978a	
Spring Migration (of adults to breeding ponds)	late March		late April	Virginia	Massey, 1990	

- 1 "Neonates" refers to newts that become sexually mature in the larval form (i.e., neoteny).
- 2 Estimated assuming temperature of 20°C using Equation 3-50 (Robinson et al., 1983) and postbreeding body weights from (a) Gill (1979); (b) Taylor et al. (1988); and (c) Gillis and Breuer (1984). The values for the larvae should be used with caution because these animals are smaller than any used to develop the allometric equations.
- 3 See Chapters 3 and 4 for methods of estimating food ingestion rates from metabolic rate and diet.
- 4 Estimated using Equation 3-26 (Whitford and Hutchinson, 1967) and postbreeding body weights from Gill, 1979.
- 5 Mean distance between capture and recapture sites, suggesting small home range size.

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2.3.7. Green Frog (true frog family)

Order Anura, Family Ranidae. These are typical frogs with adults being truly amphibious, living at the edge of water bodies and entering the water to catch prey, flee danger, and spawn (Behler and King, 1979). This profile covers medium-sized ranids. The next profile (Section 2.3.8) covers large ranids.

Selected species

The green frog (*Rana clamitans*) is usually found near shallow fresh water throughout much of eastern North America. Two subspecies are recognized: *R. c. clamitans* (the bronze frog; ranges from the Carolinas to northern Florida, west to eastern Texas, and north along the Mississippi Valley to the mouth of the Ohio River) and *R. c. melanota* (the green frog; ranges from southeastern Canada to North Carolina, west to Minnesota and Oklahoma but rare in much of Illinois and Indiana, introduced into British Columbia, Washington, and Utah) (Conant and Collins, 1991).

Body size. The green frog is a medium-sized ranid usually between 5.7 and 8.9 cm snout-to-vent length (SVL) (Conant and Collins, 1991; Martof et al., 1980). Its growing period is primarily confined to the period between mid May and mid September (Martof, 1956b). Females are usually larger than males (Smith, 1961). Adults typically weigh between 30 and 70 g (Wells, 1978). Hutchinson et al. (1968) developed an allometric equation relating green frog surface area (SA in cm) to body weight (Wt in grams):

$$SA = 0.997 Wt^{0.712}.$$

This equation also is presented in Chapter 3 as Equation 3-25.

Habitat. Adult green frogs live at the margins of permanent or semipermanent shallow water, springs, swamps, streams, ponds, and lakes (Wells, 1977). Martof (1953b) found green frogs primarily to inhabit the banks of streams. They also can be found among rotting debris of fallen trees (Behler and King, 1979; Conant and Collins, 1991). Juveniles prefer shallower aquatic habitats with denser vegetation than those preferred by adults (Martof, 1953b). McAlpine and Dilworth (1989) observed that green frogs inhabited aquatic habitats about two-thirds of the time and terrestrial habitats the remaining time. Similarly, Martof (1953b) found that the green frog relies on terrestrial habitats for feeding and aquatic habitats for refuge from desiccation, temperature extremes, and enemies. Ponds used by green frogs are usually more permanent than those used by other anuran species (Pough and Kamel, 1984).

Food habits. Adult *R. clamitans* are terrestrial feeders among shoreline vegetation. They consume insects, worms, small fish, crayfish, other crustaceans, newts, spiders, small frogs, and molluscs. Stewart and Sandison (1973) found that terrestrial beetles often are their most important food item but noted that any locally abundant insect along the shoreline may be consumed in large numbers. There is a pronounced reduction in food consumption during the breeding period for both males and females (Mele, 1980). During the breeding season, males spend most of their energy defending breeding territories, and

females expend their energy producing eggs (Wells, 1977). Fat reserves acquired during the prebreeding period compensate for reduced food intake during the breeding period (Mele, 1980). Jenssen and Klimstra (1966) found that green frogs consume most of their food in the spring and eat little during the winter. Food eaten in the spring, summer, and fall consists mostly of terrestrial prey, whereas winter food is composed mostly of aquatic prey (Jenssen and Klimstra, 1966). Juveniles (sexually immature frogs) eat about half the volume of food as do adults over the course of a year (Jenssen and Klimstra, 1966). Tadpoles are herbivorous (DeGraaf and Rudis, 1983). Green frogs eat their cast skins following molting; the casting of skin is frequent during midsummer (Hamilton, 1948).

Temperature regulation and daily activities. Martof (1953b) found that the green frog's activity period varies by frog size, with larger frogs being primarily nocturnal, small frogs being diurnal, and middle-sized frogs (5 to 7 cm SVL) being equally active during day and night.

Hibernation. Adult green frogs overwinter by hibernating underground or underwater from fall to spring (Ryan, 1953). Martof (1956a) observed frogs hibernating in mud and debris at the bottom of streams approximately 1 m deep. Jenssen and Klimstra (1966) noted that adults usually hibernate in restricted chambers within rock piles or beneath plant debris, while juveniles are more often found in locations with access to passing prey. The frogs begin emerging when the mean daily temperature is about 4.4°C and the maximum temperature is about 15.6°C for 3 to 4 days (Martof, 1953b). Juvenile frogs enter and exit hibernation after adult frogs (Martof, 1956a).

Breeding activities and social organization. Green frogs breed from spring through the summer, spawning at night (Smith, 1961; Wells, 1976). Female green frogs stay in nonbreeding habitat until it is time to spawn (Martof, 1956a). In preparation for breeding, males establish territories near shore that serve as areas for sexual display and as defended oviposition sites (Wells, 1977). Males establish calling sites within their territories where they attempt to attract females (Wells, 1977). Females visit male territories to mate and lay their egg masses. The masses are contained in films of jelly and are deposited in emergent, floating, or submerged vegetation; they hatch in about 3 to 6 days (Behler and King, 1979; Martof, 1956a; Ryan, 1953). Adults are solitary during nonbreeding periods (Smith, 1956).

Tadpole and metamorphosis. In the southern part of their range, green frog tadpoles metamorphose into frogs in the same season in which they hatched, while in the northern part, 1 or 2 years pass before metamorphosis (Martof, 1956b). Tadpoles that hatch from egg masses laid in the spring usually metamorphose that fall, while those hatching from summer-laid eggs typically overwinter as larvae and metamorphose the following spring (Pough and Kamel, 1984). Ryan (1953) found that most tadpoles are 2.6 to 3.8 cm SVL at the time of transformation. Those that transform in late June or early July grow rapidly, adding 1.4 to 2.0 cm SVL in the first 2 months and 0.4 to 0.7 cm SVL more before hibernation. Tadpoles that transform at approximately 3.1 cm SVL may reach between 5.0 and 5.8 cm SVL before hibernation (Ryan, 1953). Newly transformed frogs often move from lakes and ponds where they were tadpoles to shallow stream banks, usually during periods of rain (Martof, 1953b).

Home range and resources. The species' home range includes its foraging and refuge areas in and around aquatic environments. During the breeding period, the male's home range also includes its breeding territory (Wells, 1976). Martof (1953b) found that roughly 80 percent of adult frogs captured in the spring and again in the fall occupied the same home ranges.

Population density. During the breeding season, green frog densities at breeding ponds can exceed several hundred individuals per hectare (Wells, 1978). Adult male frogs space their breeding territories about 2 to 3 m apart (Martof, 1953a).

Population dynamics. Sexual maturity is attained in 1 or 2 years after metamorphosis; individuals may reach maturity at the end of the first year but not attempt to breed until the next year (Martof, 1956a,b). Most females lay one clutch per year, although some may lay two clutches, about 3 to 4 weeks apart (Wells, 1976). In natural populations, green frogs can live to approximately 5 years of age (Martof, 1956b).

Similar species (from general references)

- The river frog (*Rana heckscheri*) is slightly larger than the green frog (8.0 to 12.0 cm SVL) and is found in swamps from southeast North Carolina to central Florida and southern Mississippi.
- The leopard and pickerel frogs (*Rana pipiens* and its relatives, and *Rana palustris*) are medium sized and strongly spotted. There are four leopard frogs whose ranges are mostly exclusive from each other, but overlap with the green frog. The pickerel frog has a similar range with gaps in the upper midwest and the southeast.
- The mink frog (*Rana septentrionalis*) is only slightly smaller (4.0 to 7.0 cm) and is found on the borders of ponds and lakes, especially near waterlilies. It ranges from Minnesota to New York, north to Labrador.
- The carpenter frog (*Rana virgatipes*) is about the same size as the green frog (4.1 to 6.7 cm) and is closely associated with sphagnum bogs and grasslands. It has a coastal plain range from New Jersey to Georgia and Florida.

The bullfrog and pig frog are much larger ranid species and are covered in the next profile (Section 2.3.8).

General references

Behler and King (1979); Conant and Collins (1991); DeGraaf and Rudis (1983); Martof (1953a, b, 1956a, b); Smith (1956, 1961).

Green Frog (*Rana clamitans*)

<i>Factors</i>	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.	
Body Weight (g)	B B	49.1 ± 20.0 SD	25.5 - 103.5	New Brunswick, Canada	McAlpine & Dilworth, 1989	1	
	A M breeding	44.0 ± 10.0 SD	27.0 - 66.0	New York (<i>melanota</i>)	Wells, 1978		
	at metamorphosis	3		New York	Pough & Kamel, 1984		
Length (mm SVL)	A	54 - 102		NS	Behler and King, 1979		
	A M	79.8 ± 8.5 SD	103 maximum	s Michigan	Martof, 1956b		
	A F	80.3 ± 8.9 SD	105 maximum				
	J B	32.6	28.4 - 36.3	s Michigan	Martof, 1956b		
Metabolic Rate (kcal/kg-d)	basal:					2 3	
	A at metamorphosis	8.08 15.8			estimated estimated		
Food Ingestion Rate (g/g-d)						4	
Surface Area (cm²)	A	17			estimated	5	
	at metamorphosis	2			estimated	6	
<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location (subspecies)/Habitat (measure)	Reference	Note No.
adults: plant material Araneae Coleoptera Hemiptera Hymenoptera Diptera Ephemeroptera Mollusca Lepidoptera		10.8 12.1 32.8 12.9 14.4 6.8 5.6 5.4 2.5			New York/lake (% total volume; stomach contents)	Stewart & Sandison, 1973	7

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Green Frog

Green Frog (*Rana clamitans*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location (subspecies)/Habitat (measure)	Reference	Note No.
adults:					s Illinois/swamp, stream	Jenssen & Klimstra, 1966	
mineral	-	-	-	2.6	(% wet volume; stomach contents)		
plant	5.7	8.3	4.2	0.5			
Pulmonata	15.7	18.3	6.4	11.0			
Oligochaeta	2.1	0.8	2.3	6.4			
Amphipoda	1.2	0.1	-	4.6			
Isopoda	5.6	1.4	-	4.6			
Decapoda	-	-	4.1	-			
Julioforma	7.5	0.3	1.7	-			
Araneida	2.8	3.4	6.6	7.4			
Odonata	1.6	12.4	5.9	-			
Orthoptera	0.9	3.0	1.5	-			
Hemiptera	1.0	7.0	6.1	2.2			
Coleoptera	9.6	19.6	15.9	9.1			
Lepidoptera	25.4	7.0	25.1	-			
Diptera	6.0	5.2	4.5	10.3			
Hymenoptera	9.9	6.0	13.5	-			
Salientia	-	-	3.9	-			
<i>Population Dynamics</i>	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/ Habitat	Reference	Note No.	
Home Range Size	A B nonbreeding	0.0065 ± 0.0036 SD ha	0.0020 - 0.020 ha	s Michigan (<i>melanota</i>)/ shallow water	Martof, 1953b	8	
	A M breeding	meters shoreline: 4.0 - 6.0		New York (<i>melanota</i>)/ open nearshore areas of ponds	Wells, 1977		
	A M breeding	meters shoreline: 1.0 - 1.5		New York (<i>melanota</i>)/ densely vegetated nearshore areas of ponds	Wells, 1977		
Population Density (N/ha)	A M A F	476 567		New York (<i>melanota</i>)/ artificial pond	Wells, 1978	9	

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Green Frog

Green Frog (*Rana clamitans*)

<i>Population Dynamics</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)/ Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Clutch Size		4,100	3,800 - 4,300 1,000 - 7,000 3,500 - 4,000	s Michigan (<i>melanota</i>)/ pond New York (<i>melanota</i>)/ shallow ponds New York (<i>melanota</i>)/ shallow water	Martof, 1956a Wells, 1976 Wright, 1914	10
Clutches/Year			1 - 2	New York (<i>melanota</i>)/ shallow ponds	Wells, 1976	
Days Incubation (d)		3 - 6 3 - 5		Connecticut (<i>melanota</i>)/ shallow water New York/ponds, pools	Babbitt, 1937 Ryan, 1953	10
Age at Metamorphosis	early eggs late eggs early eggs late eggs	3 mo 10 - 12 mo 2.5 - 3 mo 11 - 12 mo	1 - 2 yrs	New England (<i>melanota</i>)/ shallow water Virginia, Carolinas/ shallow ponds s Michigan (<i>melanota</i>)/ shallow ponds	DeGraaf & Rudis, 1983 Martof et al., 1980 Martof, 1956a, b	11
Age at Sexual Maturity (yr)	A M A F B	1 - 2 1 - 2 1		s Michigan (<i>melanota</i>)/ shallow ponds New York (<i>melanota</i>)/ pond	Martof, 1956a, b Wells, 1977	

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Green Frog

Green Frog (*Rana clamitans*)

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Mating/Laying	May May early June	early June	mid-August September mid-August	s Michigan (<i>melanota</i>) Illinois (<i>melanota</i>) New York	Martof, 1956a Smith, 1961 Wells, 1976	
Meta-morphosis eggs laid early	early August	August, September	late September	s Michigan (<i>melanota</i>) New York	Martof, 1956b Pough & Kamel, 1984	12 12
eggs laid late	early June	next spring	mid-July	s Michigan (<i>melanota</i>) New York	Martof, 1956b Pough & Kamel, 1984	13 13
Hibernation	Oct. - Nov. Oct.		March - April late March	s Michigan (<i>melanota</i>) New York	Martof, 1956a Ryan, 1953	

- 1 Weight at metamorphosis can vary by two to four times between the smallest and largest individuals.
- 2 Estimated assuming temperature of 20°C using Equation 3-50 (Robinson et al., 1983) and body weights from McAlpine and Dilworth (1989).
- 3 Estimated assuming temperature of 20°C using Equation 3-50 (Robinson et al., 1983) and body weights from Pough and Kamel (1984).
- 4 See Chapters 3 and 4 for methods of estimating food ingestion rates from metabolic rate and diet.
- 5 Estimated using Equation 3-25 (Hutchinson et al., 1968) and body weights from McAlpine and Dilworth (1989).
- 6 Estimated using Equation 3-25 (Hutchinson et al., 1968) and body weights from Pough and Kamel (1984).
- 7 Season not specified.
- 8 Daily activity range of nonbreeding frogs.
- 9 Frogs were initially hand-captured and placed in pond; the numbers given are for those frogs that stayed.
- 10 Cited in DeGraaf and Rudis (1983).
- 11 Eggs laid before June.
- 12 Metamorphosed in the same year eggs were laid.
- 13 Metamorphosed the year following the season the eggs were laid.

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2.3.8. Bullfrog (true frog family)

Order Anura, Family Ranidae. These are typical frogs with adults being truly amphibious. They tend to live at the edge of water bodies and enter the water to catch prey, flee danger, and spawn (Behler and King, 1979). This profile covers large ranids. Medium-sized ranids are covered in the previous profile (Section 2.3.7).

Selected species

The bullfrog's (*Rana catesbeiana*) natural range includes the eastern and central United States and southeastern Canada; however, it has been introduced in many areas in the western United States and other parts of North America. It is continuing to expand its range, apparently at the expense of several native species in many locations (Bury and Whelan, 1984). There are no subspecies for the bullfrog.

Body size. The bullfrog is the largest North American ranid. Adults usually range between 9 and 15 cm in length from snout-to-vent length (SVL) and exceptional individuals can reach one half kilogram or more in weight (Conant and Collins, 1991; Durham and Bennett, 1963). Males are usually smaller than females (Smith, 1961). Frogs exhibit indeterminate growth, and bullfrogs continue to increase in size for at least 6 years after metamorphosis (Durham and Bennett, 1963; Howard, 1981a). Hutchinson et al. (1968) developed an allometric equation relating bullfrog surface area (SA in cm) to body weight (Wt in grams):

$$SA = 0.953 Wt^{0.725}.$$

This equation also is presented in Chapter 3 as Equation 3-24.

Habitat. Adult bullfrogs live at the edges of ponds, lakes, and slow-moving streams large enough to avoid crowding and with sufficient vegetation to provide easily accessible cover (Behler and King, 1979). Small streams are used when better habitat is lacking (Conant and Collins, 1991). Bullfrogs require permanent bodies of water, because the tadpoles generally require 1 or more years to develop prior to metamorphosis (Howard, 1981b). Small frogs favor areas of very shallow water where short grasses or other vegetation or debris offer cover (Durham and Bennett, 1963). Larger bullfrogs seem to avoid such areas (Durham and Bennett, 1963). Tadpoles tend to congregate around green plants (Jaeger and Hailman, 1976, cited in Bury and Whelan, 1984).

Food habits. Adult *R. catesbeiana* are indiscriminate and aggressive predators, feeding at the edge of the water and among water weeds on any available small animals, including insects, crayfish, other frogs and tadpoles, minnows, snails, young turtles, and occasionally small birds, small mammals, and young snakes (Behler and King, 1979; DeGraaf and Rudis, 1983; Korschgen and Baskett, 1963). Bullfrogs often focus on locally abundant foods (e.g., cicadas, meadow voles) (Korschgen and Baskett, 1963). Crustaceans and insects probably make up the bulk of the diet in most areas (Carpenter and Morrison, 1973; Fulk and Whitaker, 1968; Smith, 1961; Tyler and Hoestenbach, 1979). Bullfrog tadpoles consume primarily aquatic plant material and some invertebrates,

but also scavenge dead fish and eat live or dead tadpoles and eggs (Bury and Whelan, 1984; Ehrlich, 1979).

Temperature regulation and daily activities. Bullfrogs forage by day (Behler and King, 1979). They thermoregulate behaviorally by positioning themselves relative to the sun and by entering or leaving the water (Lillywhite, 1970). In one study, body temperatures measured in bullfrogs during their normal daily activities averaged 30°C and ranged from 26 to 33°C (Lillywhite, 1970). At night, their body temperatures were found to range between 14.4 and 24.9°C (Lillywhite, 1970). Tadpoles also select relatively warm areas, 24 to 30°C (Bury and Whelan, 1984). Despite this narrow range of temperatures in which bullfrogs normally maintain themselves, they are not immobilized by moderately lower temperatures (Lillywhite, 1970). The metabolic rate of bullfrogs increases with increasing body temperature. Between 15 and 25°C, the Q_{10} for oxygen consumption is 1.87; between 25 and 33°C, the Q_{10} is 2.41 (Burggren et al., 1983).

Hibernation. Most bullfrogs hibernate in mud and leaves under water beginning in the fall, but some bullfrogs in the southern states may be active year round (Bury and Whelan, 1984). They emerge sometime in the spring, usually when air temperatures are about 19 to 24°C and water temperatures are at least 13 to 14°C (Wright, 1914; Willis et al., 1956). Bullfrogs emerge from hibernation later than other ranid species (Ryan, 1953).

Breeding activities and social organization. Bullfrogs spawn at night close to shorelines in areas sheltered by shrubs (Raney, 1940, cited in DeGraaf and Rudis, 1983). The timing and duration of the breeding season varies depending on the location. In the southern states, the breeding season extends from spring to fall, whereas in the northern states, it is restricted to late spring and summer (Behler and King, 1979). Males tend to be territorial during the breeding season, defending their calling posts and oviposition sites (i.e., submerged vegetation near shore) (Howard, 1978b; Ryan, 1980). Female visits to the pond tend to be brief and sporadic (Emlen, 1976). Some males mate with several females whereas others, usually younger and smaller males, may not breed at all in a given year (DeGraaf and Rudis, 1983). Females attach their eggs, contained in floating films of jelly, to submerged vegetation (Behler and King, 1979). Adults are otherwise rather solitary occupying their own part of a stream or pond (Smith, 1961).

Tadpole and metamorphosis. Eggs hatch in 3 to 5 days (Clarkson and DeVos, 1986; Smith, 1956). Temperatures above 32°C have been shown to cause abnormalities in tadpoles and above 35.9°C to kill embryos (Howard, 1978a). Tadpole growth rates increase with increasing oxygen levels, food availability, and water temperature (Bury and Whelan, 1984). Tadpole gill ventilation at 20°C can generate a branchial water flow of almost 0.3 ml/g-min (Burggren and West, 1982). Metamorphosis from a tadpole to a frog can occur as early as 4 to 6 months in the southern parts of its range; however, most tadpoles metamorphose from 1 to 3 years after hatching, depending on latitude and temperature (DeGraaf and Rudis, 1983; Martof et al., 1980).

Home range and resources. The species' home range includes its foraging areas and refuges in and around aquatic environments. Home range size decreases with increasing bullfrog density, and males tend to use larger home ranges than females (Currie and Bellis, 1969). Bullfrogs tend to stay in the same pools throughout the summer months

if the water level is stable (Raney, 1940, cited in DeGraaf and Rudis, 1983). During the breeding season, adult males establish territories that they defend against conspecific males (Emlen, 1968). During the non-breeding season, Currie and Bellis (1969) found no evidence of territorial defense. Males often do not return to the same pond the following spring (Durham and Bennett, 1963).

Population density. During the breeding season, each breeding male may defend a few meters of shoreline (Currie and Bellis, 1969; Emlen, 1968). The densities of females and non-breeding males vary with time of day and season and are difficult to estimate. Tadpoles can be present locally in extremely high densities (Cecil and Just, 1979).

Population dynamics. Sexual maturity is attained in about 1 to 3 years after metamorphosis, depending on latitude (Howard, 1978a; Raney and Ingram, 1941, cited in Bury and Whelan, 1984). Only females that are at least 2 years past metamorphosis mate during the early breeding season; males and females 1 year past metamorphosis may breed during the later breeding periods (Howard, 1978a, 1981b). Also, some older females have been observed to mate and to lay a second clutch during the later breeding period (Howard, 1978a). Willis et al. (1956) estimated the minimum breeding length for females in Missouri to be 123 to 125 mm SVL. Mortality of tadpoles is high (Cecil and Just, 1979), and adult frogs are unlikely to live beyond 5 to 8 years postmetamorphosis (Howard, 1978b). In some areas, snapping turtles may be responsible for a large component of adult bullfrog mortality (Howard, 1981a).

Similar species (from general references)

- The pig frog (*Rana grylio*) is smaller than the bullfrog (8 to 14 cm) and is found in south South Carolina to south Florida and south Texas.

The remaining ranid species are more similar in size to the green (or bronze) frog. See Section 2.3.7 for a description of these frogs.

General references

Behler and King (1979); Bury and Whelan (1984); Conant and Collins (1991); DeGraaf and Rudis (1983); Smith (1961).

Bullfrog (*Rana catesbeiana*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>	
Body Weight (g)	B B	142.8 ± 77.4 SD	9.5 - 274.0	New Brunswick, Canada	McAlpine & Dilworth, 1989	1	
	A B	249		central Arkansas	McKamie & Heidt, 1974		
	young tadpole	2.0 ± 1.1 SD		Kentucky	Viparina & Just, 1975		
	1-yr tadpole	35.7 ± 5.2 SD					
	post-emergence:						
	1 month	18	13 - 42	Louisiana/lab	Modzelewski & Culley, 1974	2	
	2 months	30	19 - 52				
	3 months	42	27 - 77				
	4 months	56	41 - 101				
	at metamorph.	9	total length: (84 mm)	east central Illinois	Durham & Bennett, 1963		
	1 yr B	91	(240 mm)				
	2 yr B	210	(307 mm)				
	3 yr B	240	(320 mm)				
	4 yr B	260	(335 mm)				
	5 yr B	290	(348 mm)				
	6 yr B	360	(356 mm)				
Metabolic Rate (IO ₂ /kg-d)	tadpole, 25°C	2.6 ± 0.2 SE		NS/lab	Burggren et al., 1983	3	
	adult resting, 5°C	1.0	0.31 - 2.3	NS/NS	Hutchinson et al., 1968	4	
Metabolic Rate (kcal/kg-d)	basal: 2 mo (30 g) 1 yr (91 g) B B (143 g) A B (249 g)	9.1 7.0 6.3 5.5			estimated	5	

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Bullfrog

Bullfrog (*Rana catesbeiana*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Food Ingestion Rate (g/g-d)	(13 - 42 g) (18 - 52 g) (28 - 77 g) (40 - 100 g)	0.071 0.059 0.040 0.033			Louisiana (24 - 27°C)	Modzelewski & Culley, 1974	
Surface Area (cm ²)	2 mo (30 g) 1 yr (91 g) B B (143 g) A B (249 g)	11 25 35 52				estimated	6
<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
adults: Decapoda-Astacidae Lepidoptera Coleoptera (Lampryidae) (Chrysomelidae) (Carabidae) Pulmonata-Zonitidae Chilipoda sand, rock, gravel		47.7 19.0 16.0 (5.8) (5.8) (4.1) 8.3 7.7 1.2			Kentucky/NS (% wet volume; stomach contents)	Bush, 1959	
adults: plant animal (Odonata) (Coleoptera) (Hemiptera) (Hymenoptera) (Amphibia) unaccounted		19.7 65.2 (8.8) (15.8) (0.5) (2.2) (26.4) 15.1			New York/mountain lake (% volume; stomach contents)	Stewart & Sandison, 1973	

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Bullfrog

Bullfrog (*Rana catesbeiana*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
adults:					Missouri/bait minnow pond	Corse & Metter, 1980	
frogs	35	33	39		(number of items found; stomach contents)		
tadpoles	8	11	0				
shiners	305	157	25				
other fish	7	2	5				
Gastropoda	55	70	26				
crayfish	22	162	18				
other crustacea	71	42	47				
Arachnida	3	23	3				
Coleoptera (adult)	31	33	15				
Diptera (larvae)	2	7	0				
Hemiptera	41	43	16				

<i>Population Dynamics</i>	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Home Range Size (m radius)	A M nonbreed A F nonbreed	2.9 2.4	0.76 - 11.3 0.61 - 10.2	Ontario, Canada/pond	Currie & Bellis, 1969	
	A M territory	2.7		Michigan/pond	Emlen, 1968	7
Population Density (N/ha)	B B (1960) B B (1961) tadpoles: November March May	1,376 892 130,000 69,000 16,000		Ontario, Canada/pond Kentucky/pond	Currie & Bellis, 1969 Cecil & Just, 1979	
Clutch Size		7,360 ± 741.7 SE	10,000 - 20,000	Kansas/NS New Jersey/pond	Smith, 1956 Ryan, 1980	
Clutches/Year	93% of F 7% of F	1 2		Michigan/pond	Emlen, 1977	
Days to Hatching		2 - 4 4 - 5		Arizona, California/river Kansas/NS	Clarkson & DeVos, 1986 Smith, 1956	

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Bullfrog

Bullfrog (*Rana catesbeiana*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Age at Metamorphosis	B B B B	1 yr 1 - 2 yr 2 - 3 yr 3 yr		Carolinas, Virginia/NS Michigan/pond New York/NS Nova Scotia, Canada/NS	Martof et al., 1980 Collins, 1979 Ryan, 1953 Bleakney, 1952	8
Age at Sexual Maturity	M F B	1 yr after metam. 1 - 2 yr after metam. 1 - 2 yr after metam.		Michigan/pond New York/NS	Howard, 1978a Ryan, 1953	
Annual Mortality Rates (%)	A M 1 - 2 yr A M 2 - 3 yr A M 3 - 4 yr A M 4 - 5 yr	58 58 48 77		Michigan/pond	Howard, 1984	
Mortality Rates (%)	tadpoles (to metamorph.)	85.5	82.4 - 88.2	Kentucky/shallow ponds	Cecil & Just, 1979	
Longevity (yr)	A B		up to 5 - 8	Michigan/ponds	Howard, 1978b	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/Laying	February April May late May	May late June July	October late June August July	southern range in N America California, Arizona Missouri northern range in N America	Behler & King, 1979 Clarkson & DeVos, 1986 Willis et al., 1956 DeGraaf & Rudis, 1983; Behler & King, 1979	
Metamorphosis	August March June July	(1st clutch) (2nd clutch) late June-Aug.	October April early October Sept., October	California, Arizona California, Arizona Missouri New York	Clarkson & DeVos, 1986 Clarkson & DeVos, 1986 Willis et al., 1956 Ryan, 1953	

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Bullfrog

Bullfrog (*Rana catesbeiana*)

<i>Seasonal Activity</i>	Begin	Peak	End	Location	Reference	Note No.
Hibernation	late October mid-October		late March March	east central Illinois Missouri	Durham & Bennett, 1963 Willis et al., 1956	

- 1 Mean snout-to-vent length (SVL) of frogs was 98 mm SVL and the range was 45 to 128 mm SVL.
- 2 Age postmetamorphosis; maintained at a temperature of 24 to 27 °C and fed mosquitofish, crickets, and earthworms.
- 3 Restrained, cannulated; weight 5.7 g.
- 4 Mean weight of frogs was 74.8 g.
- 5 Estimated assuming temperature of 20 °C using Equation 3-50 (Robinson et al., 1983). Body weights (1) for 2-month postmetamorphosis frog from Modzelewski and Culley (1974); (2) for a 1-year postmetamorphosis frog from Durham and Bennett (1963), Farrar and Dupre (1983); (3) for both juveniles and adults of both sexes, McAlpine and Dilworth (1989); and (4) for adults of both sexes, McKamie and Heidt (1974).
- 6 Estimated using Equation 3-24 (Hutchinson et al., 1968) and body weights as described in note 5.
- 7 Based on average distance between frogs.
- 8 Cited in Bury and Whelan (1984).

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Bullfrog

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